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THE UNIVERSITY OF ALBERTA

AN INTERACTIVE SIMULATION SYSTEM FOR STUDY OF SPATIAL DYNAMICS IN COMMUNITY ECOLOGY

by

© M. DUBREUIL

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Supervisor

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DATE 26 July 1976

A maman, papa et Erman

ABSTRACT

Computer simulation can be of considerable assistance in the inclusion of space as a variable in ecological systems. In Chapter 2, the major concepts of ecology and ecological modeling are defined. Simulation is then considered as a tool for studying ecological models. Chapter 3 reviews in detail spatial dynamics in community ecology. Examples from the literature are given.

The fourth chapter describes ECOSIM, which allows a user to model the behavior of an ecological community in both time and space. The distribution, mobility, breeding, predation, and hunger characteristics of each species can be specified. Selective barriers to mobility can be established. Model definition, simulation monitoring, and editing facilities are provided. Compact but extendable data structures are employed. Output capabilities include graphical display of the simulation space and the option of plotting the population of given species against time. States of the model can be stored and later retrieved for a new simulation run.

In the final chapter, a simulation study illustrating some features of the system is presented, the system is evaluated, and some improvements to it are suggested. An Appendix contains a User's Manual.

RESUME

La simulation par ordinateur peut facilement permettre l'inclusion d'une variable "espace" dans un système écologique. Au chapitre 2, les concepts majeurs en écologie et modèles écologiques sont définis. La simulation comme instrument pour l'étude de modèles écologiques est analysée. Le chapitre 3 revoie le principe de dynamique de l'espace en écologie des communautés.

Le quatrième chapitre décrit ECOSIM, un système qui permet à un usager de modeler le comportement d'une communauté écologique dans le temps et dans l'espace. Les caractéristiques de chaque espèce telles que mobilité, reproduction, prédation, et satiété peuvent être spécifiées. Des barrières peuvent être établies pour prévenir la mobilité. L'usager peut définir et éditer son modèle et contrôler la simulation. Les données sont structurées de façon compacte mais extensible. Les résultats sont illustrés entre autres par un schéma de l'environnement et un graphique de la population de chaque espèce par unité de temps. Le modèle peut être mis en mémoire et plus tard utilisé pour une nouvelle simulation. Au dernier chapitre, une étude illustrant les diverses facilités du système est presentée, celui-ci est évalué et des suggestions sont émises pour l'améliorer. Un Manuel d'Usager est inclus en Appendice.

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CHAPTER 1

INTRODUCTION

The methodologies of differential equations and statistics have been widely used to study population growth in ecological systems. Multi-species or community growth has also been studied using statistical methods, but without much success because of the proliferation of relevant parameters (Bartlett, 1973). As May (1976) observes, one of the most efficient ways to study multi-species environments is to build a model including parameter values based on observation or intuition and then use a computer to simulate the dynamics of the system.

Work has also been done on the patterns of organisms at one moment in time (Pielou, 1969) but so far little progress has been made, even for single species populations, towards combining the study of how populations vary in time and in space. By modeling a two-dimensional environment, computer simulation can be of considerable assistance in the inclusion of space as a variable in ecological systems.

ECOSIM is an interactive programming system for use in the simulation of spatial dynamics in community ecology. It allows a user to model the behavior of a community of species in both time and space. The environment is represented as an unbounded two-dimensional grid of hexagonal cells. The user can specify predation, mobility, breeding, and hunger characteristics for any number of

species.

In the next chapter, the major concepts of ecology and ecological modeling are defined. Simulation is then considered as a tool for studying ecological models. Chapter 3 reviews in detail spatial dynamics in community ecology. Dispersion, aggregation and space-time interactions are discussed. Examples from the literature are given.

ECOSIM is the subject of Chapter 4. The system is briefly described and the characteristics of the main modules are defined. The required data structures are presented in detail. There follows a definition of the main variables included in the model, and their use. The system requirements are then described and an evaluation of its performance is given. Chapter 5 describes how ECOSIM is used to simulate a real-life problem, the system is evaluated and improvements to it are suggested. A User's Manual is included in the Appendix to provide detailed information on the use of the system.

CHAPTER 2

MODELING AND SIMULATION IN ECOLOGY

2.1 ECOLOGICAL MODELS

2.1.1 Introduction

From the Greek word oîkos ("house"), ecology is the biological discipline studying the relationship between organisms and environment (Sacchi & Testard, 1971). The problem of distribution and abundance of organisms is also of great interest to biologists (Krebs, 1972). the environment comprises the physical, chemical, and biological characteristics of the surroundings.

Populations have been studied since the 19th century. In 1798, Malthus published the first book on demography. He studied the relationship between increase in population of organisms and increase of food supply. Some of the questions he raised remain unanswered today.

Attempts to define mathematical relationships between organisms and environment have been partly successful. The classic work is that of Lotka and Volterra in 1926 (Volterra, 1937). Although many ecologists have criticized their theory as simplistic and inadequate, the approach is still widely used. Inclusion of stochastic variates has contributed to the realism of more recent formalizations.

The growth of a species can be studied either as a single isolated population or within a collection of

populations in an environment, a community.

2.1.2 Population Ecology

A population can be defined as a group of organisms of the same species occupying a particular space at a particular time (Krebs, 1972), or as isolated units of interbreeding individuals (Emlen, 1973). Population ecology has been extensively studied since the work of Lotka and Volterra. Methods to estimate population growth, for example, or prey-predator interactions are numerous. The basic parameters of a population include density, birth rate, death rate, immigration, emigration, and age distribution. With a variety of methods one can estimate the present or past values of these parameters. But the main purpose of the analysis is to predict phenomena such as the growth of a population or the effects of insertion of a predator in a species' environment.

2.1.2.1 Population Growth

The growth of a population can be analyzed mathematically. This section treats different techniques, the parameters involved and the way to specify values for the different variables.

Discrete deterministic growth. If we first assume that there is no overlap between successive generations, so that time can be expressed as a discrete variable (such cases exist in nature), we can express a population growth as:

$$N_{t+1} = N_t \left[1 + r(1 - N_t/K) \right]$$

where

N_{t+1} = population size at generation t+1;

N_t = population size at generation t;

r = net reproductive rate;

K = "carrying capacity of the environment", the population density that the environment can support.

The population at time t+1 will thus be the population at time t (N_t), increased or decreased by a factor determined by deaths and births (rN_t), and decreased by a factor which is a function of the density of the population (rN_t^2/K).

Continuous deterministic growth. Generations usually overlap, making differential equations more suitable for representing population growth. We must first make the following assumptions:

(1) breeding occurs uniformly throughout the year with no peaks;

(2) breeding is independent of sex and genotype;

(3) the influence of density on the rate of increase operates without time lag.

Population growth can then be expressed as:

$$dN/dt = rN\ (1 - N/K)$$

The solution of this differential equation is

$$N_t = K / (1 + e^{a-rt})$$

where a is a constant of integration defining the position of the curve relative to the origin. This type of equation

has been used to model the growth of some controlled laboratory populations, yeast and protozoa (Gause, 1934) for example, and some other species like beetles and fruit flies. But most natural populations do not seem to grow according to such equations.

Attempts were made to reduce the simplicity of the assumptions. Assuming that a change in N simultaneously affects b and d is not realistic. In reality, time lags occur. For example, a high population level at time t may produce a shortage of food at time t+1 and a diminution in the birth rate at t+2. Hassel (1975) proposed a new discrete model for population growth which takes into consideration the big density-dependence which is significant only with high population density.

It was assumed for analysis that breeding occurs continuously throughout the year with no peak. In fact, most animals have seasonal reproductive peaks so that r is not constant. Death and birth rates also vary by sex and age. The growth of a population is thus influenced by its sex and age structure. To include these factors and to be able to consider different age groups, two approaches are used: the life table and the Leslie matrix.

An example of a life table is given in Fig. 2.1. This table describes the mortality schedule of a population. The "static" life table is calculated on the basis of a cross section of a population at a specific time, while a "cohort" life table is calculated on the basis of a cohort of

organisms followed throughout life. By calculating the net reproductive rate (R), which is the expected number of female offspring to which a newborn female will give birth in her lifetime, and the mean generation time (T), which is the average age at which females produce offspring, we can determine the population growth: the population will increase by a factor of R every T years.

(1)	(2)	(3)	(4)	(5)	(6)
0	142	1000	563	0.563	1.58
1	62	437	198	0.453	1.96
2	34	239	98	0.410	2.17
3	20	141	32	0.227	2.34
4	(15.5) [1]	109	32	0.294	1.88
5	11	77	31	0.403	1.45
6	(6.5) [1]	46	32	0.696	1.11
7	2	14	0	0.000	1.50
8	2	14	14	1.000	0.50
9	0	0	--	-----	----

(1) Age (year) x;
(2) Observed number barnacles alive each year;
(3) Number surviving at start of age interval x, l_x;
(4) Number dying within age interval (x, x+1), d_x;
(5) Rate of mortality, q_x;
(6) Mean expectation of further life for animals alive at start of age x, e_x;
[1] Estimated number alive.

Fig. 2.1. Life table for the barnacle Balanus glandula at the upper shore level on Pile Point, San Juan Island, Washington (Krebs, 1972)

The Leslie method uses matrices to introduce the variable age. The structure of the model representation allows calculation of the number of individuals of each age group at every time step. Also considered is the lag

between the time of birth of an individual and the time he enters the breeding population. This method is thus convenient when a life table is available; the results are sometimes closely related to laboratory populations.

Stochastic growth. The models discussed so far were deterministic. Biological systems are more realistically treated in probabilistic terms. We can often work with the probability that a female will have a litter or that a predator will kill a prey. A simple model (Pielou, 1969), assumes that if

$B(N)$ = birth rate and $D(N)$ = death rate, then

$B(N)$ must decrease as N increases,

$$B(N) = a_1 - b_1 N \text{ and}$$

$D(N)$ must increase as N increases,

$$D(N) = a_2 + b_2 N.$$

So, for birth,

$$P(N \dashrightarrow N+1) \propto NB(N) = a_1 N - b_1 N^2,$$

and for death,

$$P(N \dashrightarrow N-1) \propto ND(N) = a_2 N + b_2 N^2.$$

Thus

$$dN/dt = (a_1 - a_2) N - (b_1 + b_2) N^2.$$

Even though stochastic models are more realistic, the introduction of more variables makes the analysis very difficult.

Most of the models described above predicted life cycles of some populations of simple organisms. But factors like large numbers of species, the uniqueness of each

individual and its continual adaptation to the environment, immigration and emigration, territorial behavior, and climatic fluctuations were not considered.

2.1.2.2 Species Interaction

There are three types of interaction between two species. Predator-Prey relationships (+,-) occur when the growth rate of the predator species is increased by the occurence of the prey species and inversely. If the Lotka-Volterra equations are used many unrealistic assumptions must be made. Age and sex differences are again ignored. The effects of interactions between species are instantaneous. The system is closed. Despite these restrictions, good results have been obtained, but mostly for laboratory populations.

Competition (-,-) occurs when the growth rates of the two populations are depressed by the co-occurence of the two species. If the animals belong to the same species the competition is intraspecific; interspecific competition exists between different species. Equations describing this phenomenon fit only a few laboratory populations. Transferring the results of laboratory work to field populations has proven difficult.

When both growth rates are increased by the cooccurence of the two species, the relationship is mutualistic or commensal (+,+). Commensalism is "the relationship between two organisms when one is benefited" (Emlen, 1973, p.319).

The equations for competition remain valid for commensalism and mutualism. These relationships can be treated as negative competition.

2.1.2.3 Population Regulation

In reality, the growth potential of a species is never reached. Ecologists thus believe in some form of regulation to allow for more food and more shelters and less attraction for predators. This mechanism is not considered voluntary but a consequence of two types of limiting factors: density dependent factors, which are inversely related to population size, and density independent factors. Changes in the environment, availability of resources, predation, space and spacing and social factors like crowding all contribute to population regulation and are not independent of each other. There has not yet been any attempt to introduce parameters to account for all of these factors in a system.

Fluctuation frequently occurs in population growth. Although fertility and survival rates are the main causes, delayed density dependent response and predator-prey interaction also influence the stability of a population.

2.1.3 Community Ecology

It is difficult to adequately represent an environment for a given population. The huge number of parameters and the fact that the populations coexist with many other species complicate the process. "The step up to three

dimensions introduces not only a confusing proliferation of parameters, but also a qualitative change in the dynamical complexity" (May, 1976, p.69).

2.1.3.1 Mathematical Representation

A community is an association of interacting individuals living together in the same environment. Mathematical analyses of population growth within a community are rare. The system is usually represented by a generalization of the Lotka-Volterra equations. For example, a community of competing species could be described as (Pianka, 1976)

$$dN_i/dt = r_i N_i \left(K_i - N_i - \sum_{j \neq i}^{n} \alpha_{ij} N_j\right)/K_i$$

where

n = number of species;

r_i = rate of increase of species i;

K_i = carrying capacity of species i;

N_i = population density of species i;

α_{ij} = competition coefficient.

Although the Lotka-Volterra equations have many flaws, they do provide a conceptual framework. Progress has been made towards defining population growth in a community. But most analyses of such systems are still qualitative rather than quantitative.

2.1.3.2 Species Diversity and Abundance

One of the most important properties of a community is the number of species it contains. This number should contribute to a measure of the "diversity" of the community. But if one species present in the community is much more numerous than another, this disparity should be reflected in a diversity index. An example of such an index is the Shannon-Wiener "entropy" measure:

$$H' = -\sum_{i=1}^{s} p_i \log(p_i) \text{ units,}$$

where p_i is the proportion of the i'th species in the community and s is the number of species. p_i can be the proportion of trees or animals or, in the case of plants, the relative weight of each species.

Most ecologists agree that there exists a relationship between the diversity of a community and its stability. In theory, a diverse community "ought" to be stable. If there are many prey for a single predator, the predator population will less likely go extinct, and no prey population will grow indefinitely since there are many predator species.

But it is not yet known how many species can coexist in a given environment. Two processes are involved. The number of species tends to decrease with competitive exclusion. Gause (1934) has observed that "...as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its

competitor". On the other hand, the number of species tends to increase with immigration and evolution.

A dominant species is one which is highly successful ecologically and has a great influence on the growth of the other species (Krebs, 1972). Dominance is thus related to the concept of species diversity. Although dominant species in a community are usually assumed to be ecologically constant, it happens frequently that a dominant species is largely a matter of chance events. Hence no mathematical model exists to cope with dominance.

2.2 SIMULATION

2.2.1 Introduction

It is often difficult to analyze complex dynamic systems by means of mathematics. Equations describing changes in behavior may be intractable, or mathematical formulations may not exist at all. The complexity of large-scale, real-life situations contributes to the oversimplification or lack of understanding responsible for most failures in attempting to mathematically define natural systems.

Simulation can be used to analyze problems which are too complex to be defined or solved in terms of mathematics only. There are dozens of books on simulation and each of them has its own definition of the subject. Merging the concepts together, the following was obtained.

A system is a set of entities united by some form of interaction or interdependence (Mize, 1968). There are natural systems and artificial systems. A system is open if it can exist only in a particular environment and adaptive if it reacts to changes in environment. A model is an abstraction or a representation of a real world system. A simulation is the process of reproducing the system behavior using the model. A model can then be a system of equations and a simulation would be used to solve that system on a computer. This is referred to as a "mathematical" model, or as Hall and Day (1977) call it, an "analytical" model. While modelling establishes the relationship between a real system and its model, simulation deals mainly with the relationship between the computer and the model (Zeigler, 1976).

2.2.2 Computer Simulation

The first step in studying a system by computer is to build a model. This model is specified by "a set of variables representing the principal features of the real-life system and a set of computer instructions representing the laws or decision rules that determine how these features are modified as time progresses" (Smith, 1968). The systems involved may be of business, economic, social, biological, physical, or chemical type. A model is replicatively valid if it adequately reproduces the behavioral data from the real world system. A predictively valid model is one which

can accurately predict the future behavior of the real system. The use of simulation can make the model easier to understand, and can provide hints as to the causes and effects of the process. Simulation usually speeds up the analysis, provides a basis for system modifications, and facilitates experimental manipulation. Guides can be provided for predictions and forecasting. Control is possible over the time scale and sources of variation. The model will then enable the modeller to learn how change in state occurs, and to predict and control changes.

A model can be deterministic or stochastic. It is deterministic when all entities bear fixed mathematical or logical relationship to each other (Fishman, 1973). When the future is influenced by factors whose effect cannot be foreseen exactly, the model is stochastic. We can then describe the relationships between cause and effect with probabilities.

A model is static if it does not involve time. It is dynamic when time is included as a variable. There are continuous time models (such as those based on differential equations), discrete-event models and discrete-time models (Zeigler, 1976). A continuous time model is used when changes in the states of the model occur continuously as time evolves. In a discrete-time model, a "clock" is simulated and used to count time. In a discrete-event model, even though time flows continuously, state changes can occur only in discontinuous jumps. A model is time

varying if time enters explicitly as an argument of the rules of interaction. Otherwise, the model is time invariant.

2.2.3 Programming Considerations

The construction of a computer simulation involves the following steps (Emshoff and Sisson, 1970; Ziegler, 1976):

1. Define the problem. Study the real system to see which factors affect it; find the appropriate time scale.
2. Analyze the data requirements and availability of sources.
3. Define the experimental frame, which "characterizes a limited set of circumstances under which the real system is to be observed or experimented with" (Ziegler, 1976, p. 30). A subset of input-output behavior of the real system is associated with the experimental frame.
4. Define the base model, which is valid in all the allowable experimental frames. The base model accounts for all the input-output behavior of the real system.
5. Create a lumped model, a subsystem of the base model which corresponds to the experimental frame of current interest.
6. Validate the model. A common validation method is to compare results from the simulation to historical data. Because the usual purpose of a model is to predict the future, results of the different simulations must, at some point, be checked with what actually happened.

7. Design simulation experiments. Specific combinations of manipulatable variables are used in the model to mimic real observations of the system.
8. Analyze the results. The simulation runs are evaluated and weaknesses are corrected if possible.

Programming a simulation touches many aspects of computing science, including creating, filing, and destroying records, searching lists, and generating random variates. Classes of objects within a system must be defined, adjustments performed as conditions within the system vary, and objects related to one another and to their common environment.

Consideration has to be given to random number generators. Random variables are used to represent factors which fluctuate in an unpredictable but statistically describable way. One can use a generator to simulate almost any discrete or continuous probability distribution.

Another concern is whether the model is interactive or not. An interactive model is one that interacts with its user. Some of the requirements for an interactive simulation package include (Sohnle, Tartar, & Sampson, 1973): a flexible command language, easy for the user to understand; graphics and output capabilities so that the user can visualize the model; user capability to specify the length of the simulation, to save and restore the results and to restart the simulation; provisions to modify the model characteristics and parameters; and painless error

recovery.

The language used for the actual coding of the simulation program needs good data structure capabilities, conditional and unconditional branch and iteration capability, and of course logical and arithmetic operations.

Engineering design, econometrics, nuclear reactor design, military operational research, and management science are all sources of models suitable for simulation. Many management systems involving queuing problems can be solved by simulation. In a queuing problem, an arrival occurs requiring a service to be performed. The system either performs the service or keeps the demand on a waiting list until it can execute it. PERT networks can also be simulated. A schedule of events or "critical path" has to be found among a specific number of activities required in order to achieve a task.

2.2.4 Applications in Ecology

Ecosystems as a whole are hard to study even by simulation because of the great number of variables to be included. Most of the simulations of ecological models in the 1960's involved small numbers of variables, and usually only one or two species. But recently, because of social pressures and attention given to ecology and resources management, ecologists have increasingly begun to simulate ecosystems. Examples of two approaches are given here.

2.2.4.1 The St Kilda Ecosystem (Milner, 1972)

St Kilda is an island, part of a National Nature Reserve in the United States. It is a simple ecosystem since there are only a few vegetation types and only one major herbivore, the soay sheep. The model was built to study mainly the sheep population and the vegetation on which they feed. The main steps of the simulation were:

1. Calculate the growth of plants as a function of the temperature and the weight;
2. Calculate the number of sheep as a function of body weight and age structure;
3. Harvest from population of sheep;
4. Calculate weight of plant material removed by sheep.

These four steps simulated one day on the island. The system was intended to predict the future number of sheep, but did not do so very successfully. The conclusion was that either the model was structurally incorrect, or that one or more of the equations were wrong or had coefficients whose values were too far from reality. But still the model improved the understanding of the system and provided useful data.

2.2.4.2 The Jabowa Model (Botkin, 1977)

Trees compete for resources: light, water, minerals, and a place to grow. If a tree grows faster, it shades its neighbors who die without light. The growth, death, and reproduction of trees are functions of light, moisture,

temperature, and nutrients. Given equations for growth as functions of these variables, the Jabowa Model simulates the growth of individual trees on small forest plots. The program is interactive and uses a screen, a keyboard, and a light pen. The user can plant or log any number of trees from different species. Time in years can be specified along with the output interval. The program can also be run in "batch" mode for long runs.

The model was tested and proven to work at least in the sense that it reproduced the general events. Simulation experiments were also undertaken to study the response of a forest to perturbations and manipulation.

CHAPTER 3

SPATIAL DYNAMICS IN COMMUNITY ECOLOGY

3.1 INTRODUCTION

The density of a population has important effects on its growth. Overcrowded areas do not contain enough resources for their inhabitants and the death rate increases. In undercrowded regions, mating might not be sufficient to insure survival. Unless all individuals are distributed evenly, the density effect will vary from place to place. Spatial heterogeneity and ability of movement thus influence species interactions and dynamics.

There are three patterns of dispersion in populations. Clumped or underdispersed populations occur when organisms are attracted to each other. The population is spaced or overdispersed if individuals repulse one another. Finally, the population can be randomly dispersed.

Space can be treated in a discrete or continuous fashion. Organisms can live in discrete habitable units, like the shoots of a tree. Or space can be considered as continuous where individuals occupy any point in space, like trees in a forest. Finally, it is sometimes impossible to delimit individuals so that they can be counted.

Studies of spatial patterns of populations of organisms have been popular in the last twenty years. Most of these studies, however, involve sessile or sedentary organisms and rarely has time be included as a variable.

Different approaches have been used to study spatial patterns in a single-species population.

Before Lloyd (1967) defined "mean crowding", the usual measure of crowding was simply the average number of individuals. Actually, factors like the spatial pattern of distribution, or the way individuals react towards each other when they meet, or even the way they move, can influence the degree of crowding. To include the spatial aspect of the dispersion of a population, Lloyd defined a measure of crowding as the mean number per individual of other individuals in the same quadrant. He also defined the measure of crowding when samples are used instead of complete data.

Hairston, Hill and Ritte (1971), sampling a field in Ann Arbor, Michigan, discovered "the failure of the sets of samples to reflect the distribution of the individual species in a satisfactory manner" (p. 343). But they also found that sampling in a grid pattern was far superior to sampling at random.

For any motile species, patterns change with time, making "dispersal" or "diffusion" studies more appropriate. Dispersal is "the apparently aimless, underdirected movements of animals that seem to be wholly random" (Pielou, 1969). Organisms disperse to find a suitable habitat. A population responds to local variation in the environment with movement of individuals between areas.

Holgate (1971), in his survey of results in random walk

theory, elaborated three models according to whether individuals have no attraction to a home base, or the attraction diminishes or increases with distance. Levin (1976) provided a general framework for modeling the dynamics of spatially distributed populations. He used a continuous time approach but the environment was subdivided into discrete islands or patches. The species density was then defined in terms of differential equations, including the intrinsic rate of increase of the species, the carrying capacity of the environment and a coefficient of diffusion.

3.2 MULTI-SPECIES SPATIAL INTERACTIONS.

If many species live in the same environment, or if they have some effect on one another, their patterns may not be independent (Pielou, 1969). By statistical analysis of a table whose entries specify the number of cells or units that contain individuals of every species, one can determine if two species are distributed independently of each other.

Murdoch (1977) studied the stabilizing effects of "switching", where a predator divides its time between two different prey areas, spending more searching time in the area that contains more prey or where the capture is more "rewarding". He came up with a model which describes the number of a given species eaten per unit time as a function of the transit time between the two areas, the time taken to "handle" the average individual of this species, the density of the prey species, the successful searching rate for the

prey species and the search time. Results from experiments with a predatory fish (guppies), a surface prey (Drosophila) and a bottom prey (tubificid worms) verified the basic assumptions of the switching model.

Investigations using simulation have also been done to study spatial behavior in predator-prey systems. The work of Huffaker provided the experimental frame and data for many of the studies.

3.2.1 Huffaker (1956,1958)

Huffaker studied the use of predators as a density control tool. Strawberry crops in California suffered heavy damage from the cyclamen mite Tarsonemus pallidus Banks unless a predatory mite, Typhlodromus cucumeris Oudemans, was present. Both field and greenhouse experiments were conducted.

A female cyclamen mite lays about three eggs per day for four or five days. Only about five per cent of the adult population is male. By controlling its reproductive rate and its searching behavior, the predator can both hold the density of the prey at levels noninjurious to the strawberry plant and also can survive at low prey density. The predator usually delays its appearance in a field until the prey is well established.

The main goal of the field and greenhouse experiments was to find a way of controlling the predator population. Sampling was used to estimate the different populations.

The conclusion was that the predators "exert very effective control of the cyclamen mite in third- and fourth-year fields in this area when their activities are not inhibited by detrimental chemical treatments used for control of other pests" (Huffaker and Kennett, 1956, p.198). For the greenhouse tests, seventy-two potted plants were arranged in two randomized groups. One group was kept predator-free and the corresponding plants rapidly died. The results from the studies suggested that deliberate infestation of new plantings by the predatory mite could be a means to achieve equilibrium and preserve the crops.

The objective of the 1958 experiments was to create an ecosystem where the predator and the prey would continue living together so that they could be studied in detail. The prey was the six-spotted mite, Eotetranychus sexmaculatus and the predator, Typhlodromus occidentalis Nesbitt, known as a voracious enemy of the six-spotted mite. Each universe consisted of a metal tray containing a ten by four array of oranges and/or rubber balls. The predators and prey were free to move onto or leave oranges or balls but not to leave or enter the universe. The utilization of rubber balls made it possible to change the total food substrate (oranges) and the degree of dispersion of that substrate. At intervals of eleven days, one quarter of the oranges (the oldest) were replaced. Sampling was used to count populations. Results were obtained both when the plant food was readily accessible, all in one location, and

when the food was widely dispersed with intervening rubber balls. Groups of prey with and without predators were included. Different areas of food were established by covering part of the oranges with paraffin and paper. Some of the results are summarized in Table 3.1. "Adjacent food" means a 2-orange feeding area on 4 adjacent oranges. "Dispersed" implies the same feeding area but dispersed in the tray. The last type of experiment used a 2-orange feeding area on 20 oranges dispersed in the tray.

Conclusions from these studies were that the environmental area must be large enough to permit co-existence of the predator and the prey, yet not so large as to limit interchange of the biotic participants. "Migration" (or, here, simple movement) is necessary to avoid extinction of either the prey or the predator. It is possible to establish complex universes, utilizing wide dispersion and also including partial barriers, in which the predator-prey coaction would not be self-annihilative.

Table 3.1. Mean prey population per orange in Huffaker experiments.

Food	Predator absent	Predator present
adjacent	4700	250
dispersed	3500	4056
alternating with balls	3300	1800

3.2.2 Murdie (1971)

Murdie suggested that the spatial distribution of prey influences the ability of predators to search successfully for food, and that adaptive behavior is shown by the attacker. A random walk search by the predator was tested with different prey density and spatial distribution using a computer-simulated model.

Some of the models describing predator-prey relationships include a coefficient of "killing efficiency", which might reflect the competition between predators or the searching ability of the attacker. For example, some predators change their pattern of searching when they encounter a prey. An intensive search around the discovery area begins, which can be fruitful if the prey are aggregated but detrimental when they are dispersed.

The environment is represented by 150 quadrats of 10x10 cells each. A quadrat is a square area of vegetation marked off for study. Using the negative binomial distribution

$$p_x = \left(\frac{k}{k + \bar{x}}\right)^k \left(\frac{\bar{x}}{\bar{x} + k}\right)^x \frac{(k + x - 1)!}{x!\ (k - 1)!}$$

where x is the mean density per quadrat, a frequency is determined ($f_x = Np_x$, where N is the number of quadrats). Different k and x values are used and a number of quadrats $[f_x]$ are each allocated x prey. The prey are either distributed at random within a quadrat or a random location is chosen in the quadrat around which the prey are clumped. Only one prey is allowed per cell. A fixed number of 200

predators are used, each of them being assigned to one quadrat at random. All predator-prey encounters resulted in a predation event. After twenty successive failures, the predator is assumed to die. For some of the runs a satiation level is set at ten prey.

Results showed that the clumped model has a lower level of predation then the non clumped model, thus suggesting that aggregation has some protective value against random walk predators. The introduction of a satiation level significantly modified results. As expected, the number of prey killed was proportional to the number of prey available. In the record of the discussions following the contribution, W.E. Waters from the U.S. Forest Service notes that prey movement should be included and Murdie himself suggests the introduction of reproduction for both predators and prey.

3.2.3 Maynard Smith (1974)

Migration is believed to have a stabilizing effect on a predator-prey system. Maynard Smith developed a model based on the following assumptions:

1. The habitat was divided into "cells" which could be considered either as a continuum or as a discontinuous habitat;
2. The effects of immigration and emigration were immediate;
3. Migration was "conservative", in that the system was

closed;

4. The environment was uniform.

By graphical analysis, Maynard Smith showed that migration cannot stabilize an unstable predator-prey system to insure coexistence. A model was built where a cell was considered as an "orange" (see Huffaker, 1958). The cell could be in eight different states: empty (E), containing few prey (HA), increasing prey (HB), many prey (HC), many prey with few predators (MA), many prey with increasing predators (MB), many prey with many predators (MC), and few prey with many predators (MD). Probabilities were defined for state transitions. The general conclusion, after the behavior of the model was analyzed by computer simulation, was that persistent coexistence of predator and prey could easily be achieved. Conditions which helped this coexistence included high level of migration and presence of refuge for prey, restriction of the migration period for the predators and a large number of cells.

3.2.4 Ziegler (1977)

Most analyses of spatial effects in ecology have employed the assumption of continuous population exchange mechanisms. Ziegler considers a system where migration can occur only at specific points in the predation cycle, such as when the prey or predator population of a cell reaches the carrying capacity of that cell (like the Maynard-Smith model). The results of his simulation are given here.

The base model (see section 2.2.3) is specified by the Lotka-Volterra equations

$$dx/dt = ax\ (1 - x) - xy$$

$$dy/dt = -by + xy$$

where

x = number of prey, y = number of predators

a = growth rate of the prey

b = death rate of the predator.

Parameters L1 and L2, the prey and predator extinction levels are defined, which encode the notion of "sufficiently large" number of organisms. A cell (lattice point of an infinite two-dimensional grid) is then defined to be locally "unstable" if $b < L1$ and $a < L2/(1-b)$.

The assumptions of the lumped model are:

1. Each cell goes through the following sequence of states: EMPTY, PREY (containing prey), PREY' (containing maximum number of prey), PRED (containing both prey and predators), PRED' (containing maximum number of predators), EMPTY.
2. Migration of prey from cell i to cell j occurs only when cell i is in PREY' state and cell j is EMPTY.
3. Migration of predators from cell i to cell j occurs only when cell i is in PRED' state and cell j is either in PREY or PREY' state.
4. Migration from cell i to cell j has no reverse influence on cell i.

When a cell enters the state PREY', the neighboring cells

are scanned and each EMPTY cell is converted into a PREY cell with probability h. In the same way, when a cell enters the state PRED', the adjacent cells in PREY or PREY' state are converted to PRED state with probability p. Simulations were run using different values for p and h and results were identical to Maynard-Smith's (see section 3.2.3). The mathematical model accounting for the results took the form of the Lotka-Volterra system and could explain the ability of an unstable system to stabilize through a discrete population exchange mechanism.

An ecosystem is usually complex and a single model to represent it, however desirable, is not practical. Ziegler (1978) suggested that partial models be built corresponding to different experimental frames and that the computer be used to integrate this collection of models into a synergistic whole. These models can be partially ordered by use of morphism relations which induce "a mapping from the parameter assignments of the finer model to those of the coarse ones" (Ziegler, 1978). As an example, Zeigler considered the universe employed by Huffaker (1958). Four related models were built representing different refinement levels. The first (base) model was of stochastic differential equation type and represented one local state (situation on each patch). The second (lumped) model, of stochastic discrete event type, kept track of the same variables as the first model but updated them only at "event times". The third model ("occupancy") is an abstraction of

the second model in which a small number of states was used to represent the local situation. The fourth model ("random phase-space") described the global behavior of the third model.

All the models could qualitatively explain the observed persistence in Huffaker's universes and the "more refined models were able to give close quantitative agreement as well" (Ziegler, 1978).

CHAPTER 4

ECOSIM

4.1 INTRODUCTION

A system called ECOSIM has been developed to interactively simulate ecological phenomena on a digital computer. ECOSIM allows a user to model and simulate the behavior of a community of many species in both space and time. The program is capable of handling large "ecosystems" including numerous species and many individuals. Easy to operate, ECOSIM's usage requires no knowledge of computers. A dialogue is established with the user to allow him to build his model. For each species, questions are asked about its different characteristics and parameter values. Choices are given for output intervals. Simulations can be run on previously saved or newly created models. Editing facilities are provided so that between runs, the user can alter the environment in any desired way. The main features and options of the system are outined below.

Hexagonal tesselation. The environment is represented as an unbounded two-dimensional grid of hexagonal cells. The hexagonal element is preferable to a square or triangle because it has six unambiguous neighbors and permits better approximation to arbitrary delineations. Each cell can contain 0, 1 or more individuals and/or 0, 1 or more barriers (to be defined later).

Species and individuals. Any number of species can be included in the model. Any number of individuals can belong to each species. The only practical limitation on the size of the simulated ecosystem is imposed by the availability and cost of computer resources.

Initial distribution. After specifying the initial number of individuals for a species, the user either enters their locations (as coordinates) or selects parameters for a stochastic distribution (uniform, normal, exponential, or Poisson).

Processing level. A processing level is associated with each species. Processing levels determine the order in which species are processed during a time step, individuals of the motile species with the lowest processing level moving first.

Mobility. A mobility factor determines the probability of each individual of a (motile) species of moving in any time step. The mobility factor can be dependent on the hunger level if the user wishes. If so, parameters of the quadratic equation for the curve passing through (MIN,1), (MED,MOB), and (MAX,0) are determined, where MIN is the minimum satiety level (to be defined later), MAX is the maximum satiety level, MED is the middle point between them, and MOB is the mobility coefficient. The mobility coefficient corresponding to any satiety level can be calculated from the quadratic equation.

If the mobility factor is not zero, a competition

factor determines the probability of eliminating an individual trying to occupy the same cell as another individual of the same species. If the user specifies a random walk, the occupied cell and each of its neighbors are assigned a probability of 1/7. Alternatively, the user may specify the probability of movement in each direction.

Predator-prey relationship. For each prey species, the user assigns to each predator species a probability that a predator will kill a prey, as well as the maximum number of prey a predator can kill per unit time.

Breeding specifications. For any species which is a predator and produces offspring, the user sets a breeding interval (in time units), a probability of breeding, and the mean and variance of the number of normally distributed offspring. At the expiration of the breeding interval, some new individuals may be "created" in accord with the above parameters. The offspring are randomly distributed in cells surrounding the parent. Each newborn is given the same satiety level (see below) as the parent, a breeding clock time of zero, and the species' trophic level, mobility, predator, breeding, satiety and exclusion characteristics.

Satiety specifications. The satiety of an individual is indicated by an integer value ranging from a minimum value indicating the starvation point (the individual dies) to a top value indicating the satiation level (the individual does not eat even if he encounters prey). An increment value chosen by the user is added to the satiety

level each time the predator kills a prey. A decrement value is subtracted for each time step the predator does not find a prey in its cell. For each predator species, the user sets the mean and variance for the initial (normal) distribution of satiety values.

Exclusions. The user may specify "incompatible" species. If species i excludes species j, an individual of species j will not be allowed to move into a cell occupied by an individual of species i.

Global modifications. At the end of each time step, a general function (specified by the user) can be applied to an existing species population to change the number of individuals. The global modification is specified as a Fortran expression of the form f(x,t) where x is the actual population, and t the actual time step. For example, if the user specifies 2*x*sin(t) as a global function for a given species, the population of this species will double at every time step, weighted by a factor of sin(t). If $x(t+1) < x(t)$, deletions are made at random. If $x(t+1) > x(t)$, additions of new individuals are made according to the initial distribution. If the initial distribution was expressed as specific coordinates, the user will be requested to enter as many coordinates as required for the "new" individuals. A satiety level corresponding to the satiety initial distribution is given to each individual. This feature can be used to simulate migration and seasonal variation.

Barriers. Barriers can be established either to create refuges for certain species or to impede or prevent mobility. For each barrier type, the user provides probabilities of crossing for any number of species (the default value for the probability of crossing is 1). Barriers can be distributed either at random (uniform, normal, exponential or Poisson), by specifying coordinates, or by giving the four side coordinates of a rectangle.

Output capabilities. The user can have the environment displayed graphically at any terminal. Displays are provided initially, at specified time steps, and at the end of the run. The environment is divided into windows of up to 16x16 cell regions, and the user can display all regions or only desired regions.

Editing. The user can alter the ecosystem specifications before initiating or continuing simulation. Species can be created, individuals added to or deleted from existing species, all species characteristics modified, and individuals moved from their location to new cells. In the same way, new barriers can be created, existing barriers moved or deleted, and new barrier specifications defined.

Saving and retrieving files. Before and/or after the actual simulation, the existing state of the model can be saved in a file whose name is supplied by the user. In a subsequent run, the user can request that the simulation be run using the information on the environment contained in that file.

Run. The user supplies the number of time steps, the output interval, and any stopping conditions (if a given species reaches a certain maximum or minimum value). The simulation is then carried out, using either a newly created environment or one that was previously saved, and output is produced as required.

Dialogue. The data structure needed for the simulation is built while the user is answering questions from the program. Error recovery is possible from almost any part of the system. The answers of the user can either be spelled out (like YES or BARRIER) or abbreviated with the first letter (Y or B). When an invalid answer is given, the question is usually repeated. Sometimes an explanation is given of the error if the situation is not clear. At certain points, a null answer has to be given to terminate a cycle of questions. A full description of the rules is given in the User's Manual (see Appendix). A hypothetical dialogue follows, illustrating various options of the system.

SYSTEM	USER
EXPLAIN?	NO
CREATE?	YES
SPECIES 1?	YES
DISPLAY SYMBOL:	*
PROCESSING LEVEL:	1
MOBILITY(0-1):	0
PREDATOR?	NO
EXCLUSIONS?	NO
INITIAL NUMBER:	GHI
INITIAL NUMBER:	400
RANDOM DISTRIBUTION?	YES
U, N, E, or P:	U
XMIN:	-20
XMAX:	20
YMIN:	-10
YMAX:	30
PRINT INITIAL DISTRIBUTION?	NO
GLOBAL MODIFICATIONS?	YES
FUNCTION:	
X**2+5	
SPECIES 2?	YES
DISPLAY SYMBOL:	A
PROCESSING LEVEL:	A
PROCESSING LEVEL:	2
MOBILITY(0-1):	.7

COMPETITION FACTOR (0-1):	.2
UNIFORM RANDOM WALK?	YES
PREDATOR?	YES
PREY SPECIES:	1
PROBABILITY OF KILLING:	1
MAX KILLS / UNIT TIME:	1
PREY SPECIES:	
BREEDING INTERVAL:	10
BREEDING PROBABILITY:	.85
OFFSPRING MEAN:	2
OFFSPRING VARIANCE:	1
SATIETY SCALE TOP:	10
SATIETY SCALE BOTTOM:	0
+ INCREMENT:	3
- INCREMENT:	1
SATIETY INITIAL MEAN:	5
SATIETY INITIAL VARIANCE:	.3
SATIETY DEPENDENT MOBILITY?	N
EXCLUSIONS?	YES
SPECIES NUMBER:	3
INITIAL NUMBER:	4
RANDOM DISTRIBUTION?	YES
U, N, E, OR P:	N
XMEAN:	0
XVAR:	5
YMEAN:	0
YVAR:	5

PRINT INITIAL DISTRIBUTION? ..... Y

X	Y
2	-1
-3	4
0	2
-1	-5

GLOBAL MODIFICATIONS? ..... NO

SPECIES 3? ..... Y

DISPLAY SYMBOL: ..... B

PROCESSING LEVEL: 2

MOBILITY(0-1): 1.4

MOBILITY(0-1): 4

COMPETITION FACTOR(0-1): 6

UNIFORM RANDOM WALK? ..... N

6 WALK PROB. (CLOCKWISE FROM UPPER RIGHT): 2

... .2

... .1

... .1

... .3

... .05

PREDATOR? ..... Y

PREY SPECIES: 4

PROBABILITY OF KILLING: 7

MAX KILLS / UNIT TIME: 2

PREY SPECIES: .....

BREEDING INTERVAL 15

BREEDING PROBABILITY: 1

OFFSPRING MEAN: 6.6

OFFSPRING VARIANCE: 2.5

SATIETY SCALE TOP: 100

SATIETY SCALE BOTTOM: 10

+ INCREMENT: 10

- INCREMENT: 1

SATIETY INITIAL MEAN: 35

SATIETY INITIAL VARIANCE: 0

EXCLUSIONS? ..... N

INITIAL NUMBER: 2

RANDOM DISTRIBUTION? ..... N

2 COORDINATE PAIRS:

5 3

2 3

PRINT INITIAL DISTRIBUTION? ..... N

GLOBAL MODIFICATIONS? ..... N

SPECIES 4? ..... N

BARRIER 1? ..... YES

DISPLAY SYMBOL: ..... -

SPECIES: 4

CROSSING PROBABILITY: 0

SPECIES: .....

NUMBER OF CELLS: 3

RANDOM DISTRIBUTION? ..... N

SPECIFIC (S) OR CORNERS (C)? ..... S

3 X-Y COORDINATE PAIRS:

```
$CONTINUE WITH BARR1 RETURN

BARRIER 2? ..................................... N

DESCRIBE THE ENVIRONMENT? ...................... N
SAVE, EDIT, QUIT, OR RUN? ...................... E
EDIT BARRIER, SPECIES, OR END? ................. B
ADD, DELETE, OR MODIFY A BARRIER? .............. M
WHICH BARRIER? ................................. 1
MODIFY
...DISPLAY SYMBOL? ............................. Y
DISPLAY SYMBOL ................................. +
...SPECIES/BARRIER CHARACTERISTICS? ............ N
...INDIVIDUALS? ................................ N
EDIT BARRIER, SPECIES, OR END? ................. E
SAVE, EDIT, QUIT, OR RUN? ...................... R
MAXIMUM SIZE OF GRID: .......................... 14
UNTIL WHICH TIME STEP: ......................... 20
OUTPUT INTERVAL: ............................... 5
STOPPING CONDITIONS: SPECIES: ................. 1
MIN, MAX: ..................................... 0 100
STOPPING CONDITIONS: SPECIES: ..............
   .
   .       run
   .
SAVE, EDIT, QUIT, OR CONTINUE? ................. S
FILENAME: ...................................... WORLD
```

```
RUN COMPLETE.  RESULTS DESIRED? ..............  NO
SAVE, EDIT, QUIT, OR CONTINUE? ..............  Q
RESULT FILE TO BE MADE PERMANENT? ............  NO
PRINT RESULT FILE? ...........................  Y
> *PRINT* ASSIGNED NUMBER 123456
# *PRINT* 123456 RELEASED, 12 PAGES
PLOT? ........................................  YES
SPECIES ......................................  1
SPECIES ......................................  2
SPECIES ......................................
PLOT COMPLETE
PLOT? ........................................  NO
004.56 SECONDS IN EXECUTION
#
```

4.2 System Structures

The system is composed of eight main modules including the MONITOR. A schematic diagram is shown in Fig. 4.1.

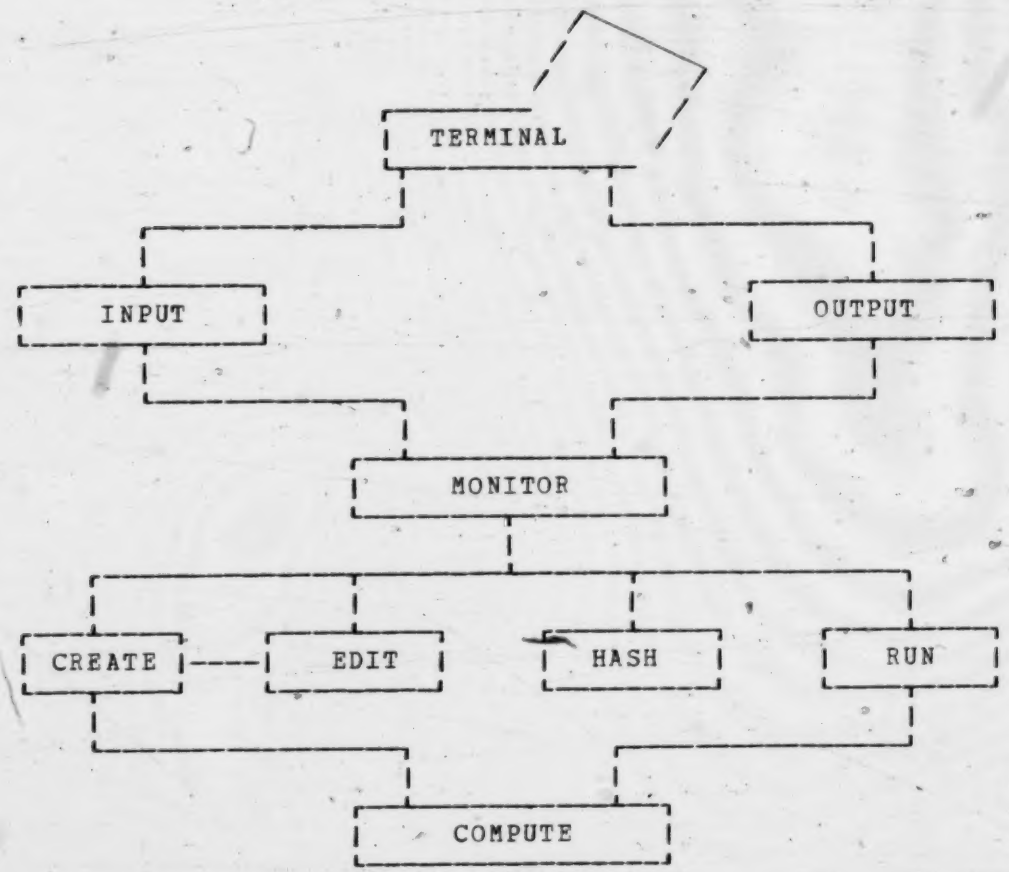

Fig. 4.1 Schematic representation of ECOSIM.

The set of records representing the data for species, barriers, predation, and exclusion characteristics is accessible from most of the modules. Each module is considered below.

4.2.1 MONITOR

The MONITOR is the control center of the simulation system. Initialisation and control of all internal operations are done in the MONITOR. The main sequence of operations is:

1. Explain
2. Create a model or get it from a file
3. Output
4. Edit, save, quit, or run
5. If edit, edit and go to 4.
6. If save, save and go to 4.
7. If run, run and go to 9.
8. If quit, quit.
9. Edit, save, quit, or continue
10. If edit, edit and go to 9.
11. If save, save and go to 9.
12. If run, run and go to 9.
13. If quit, quit.

A model can thus be saved before and after the actual simulation, allowing study of the model before further simulation is attempted. All steps (except 2) are optional. Once the user has examined the results of a simulation, he can simply restart the system, obtain the model from a file and use it to "continue" the simulation. The random number generator is initialized by the MONITOR using the computer clock as a seed. Also initialized are the default minimum x and y value and maximum x and y value. Record definitions

are given for species, individuals, barriers, barrier cells, predation, exclusion, species/barrier and halting characteristics. Pointers to the different records are set to null. Tables are created for the parsing of the global functions.

4.2.2 INPUT/OUTPUT

Several procedures are included as input/output facilities. EXPLAIN is used to refresh the user's memory of the facilities of ECOSIM. Since the information provided by EXPLAIN will not be sufficient for a new user, a user's manual is provided (see the Appendix).

The procedure CREATE initializes the main parameters and controls the "conversation" about the model between the system and the user. Questions are asked about the characteristics of the model being built and data structures are created. The procedure can be called from the MONITOR, or from EDIT if a new species or barrier is introduced in an existing model. Error recovery is done simply by repeating the question if the answer is invalid (like a real number for an integer or an illegal character in a number). Breeding and hunger characteristics are requested only if the species is a predator. A normal distribution $N(\mu,\sigma)$, where μ is the offspring mean and σ is the offspring variance is used to compute the number of offspring. If the mobility is dependent on the satiety, the coefficients of the quadratic equation corresponding to the given variables

(see Fig. 4.2) are calculated and stored. At a given time step, the individual is then moved if a number picked at random is less than $aHUN^2 + bHUN + c$ where HUN is the satiety level of the individual at this time step.

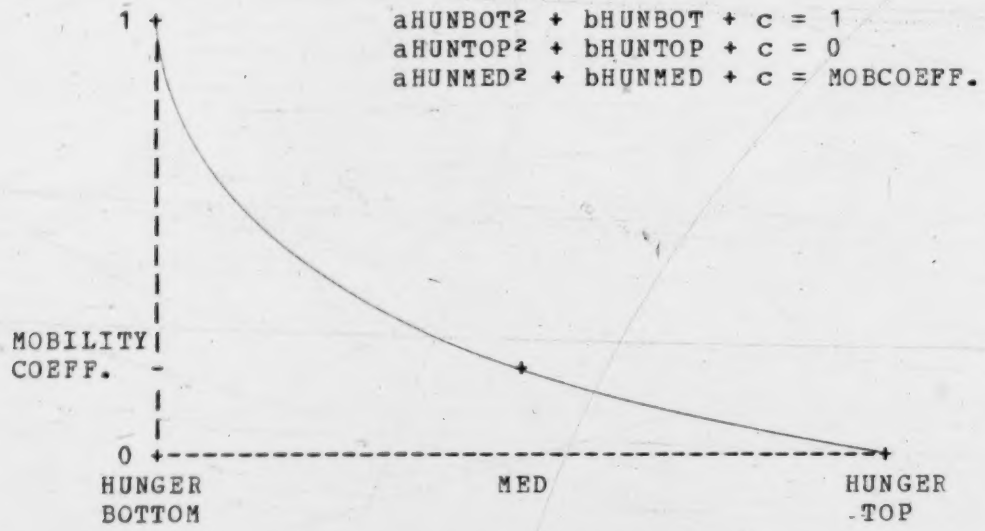

Fig. 4.2 Hunger dependent mobility curve.

To generate the individuals, the user first enters the number to be created and if they are to be placed at random. If not, the given number of individual locations is requested. The user can either enter the locations one by one or retrieve them from a file. If the individuals are to be placed at random, a distribution and parameters are chosen by the user. For each individual, two uniformally distributed random numbers (one for each coordinate) are transformed by standard procedure into numbers with the given distribution (Fishman, 1973).

If the user wishes to use a model already saved in a file, the procedure GETFILE is called which handles the creation of data structures and transfers the data from the file to the records. A check is made to see if the file exists and if not, the user is prompted for another filename.

Before or after each simulation run, the existing model can be stored in a file via SAVEFILE. The procedure goes through the data records and saves all needed information for subsequent runs. Values of important variables values like the seed for the random number generator, the number of species and barriers and the minimum x and y and maximum x and y are also stored. The hashing table is not stored since hashing is done on newly created records or on records retrieved from a file. Other procedures are used to output information about the different species and barriers, if requested.

At given output intervals, the present state of the model is displayed as windows of up to 16x16 cells in a "grid" form. Individuals and barriers are shown with their display symbol. At the beginning and at the end of each run, and also at output intervals if requested, statistics are given about the number of individuals left of every species and their characteristics.

Throughout the simulation run, results are saved in a temporary file created at the beginning of the run. Before quiting, the user can request that this file be made

permanent and/or printed on a batch printer. If the file is to be made permanent, a filename is requested and the file is stored permanently if enough space is available.

A plot option allows the user to plot the population of desired species at each time step. For each species, population versus time step is plotted on the Calcomp plotter. Each answer YES to PLOT? generates a new graph.

4.2.3 EDIT

Most of the model's parameters can be altered via EDIT. New species or barriers can be created or existing ones modified or deleted. Any general parameter of a species or a barrier can be altered. A species, for example, can become a predator or can cease to be one. Individuals or barrier cells can be moved or their characteristics changed. Predation, exclusion, and species/barrier parameters can also be modified.

4.2.4 HASH

Frequently during simulation, the contents of a given cell have to be accessed to determine what individuals or barriers it contains. A hash table is built so that, given the coordinates of a cell, a pointer runs through the data structure to every individual or barrier cell occupying the given cell (see Fig. 4.6). Before hashing is done, the size of the table is determined: the square of the longest side or 100 (whichever is less) is assigned as the size of the

table. For example, if the environment is a 5x3 cell grid, the size of the hash table will be 25 (5^2). Then the hashing function assigns an integer number to the cell (modulo the size of the table) according to its position in the environment (see Fig. 4.3). For a given coordinate pair, the corners of the "square" to which it belongs are found. For example (from Fig. 4.3) the corners for the cell (10,-1) (which corresponds to cell 16) are 10, 14, 18, and 22 (second square from the center). To find the corners, the maximum distance DIST of the cell from the center cell, i.e. the cell in the middle of the grid, is calculated. The four corners are then

```
CORNER1 = (DIST * (DIST - 1) * 4) + 2
CORNER2 = CORNER1 + DIST * 2
CORNER3 = CORNER2 + DIST * 2
CORNER4 = CORNER3 + DIST * 2
```

Finally, according to the position of the cell in the square, its distance from the appropriate corner is found which then added to the corner itself gives its hashing key. If the number is greater than the size of the table, it is divided by the size of the table and the modulo is taken.

A pointer goes from the hash table element to the first individual of the corresponding cell, and then from this individual to a next individual or barrier also occupying this cell or hashing to the same table position. The hashing function is used each time an attempt is made to move an individual, to see if there is a barrier the

	5	6	7	8	9	10	11
1	48	10	11	12	13	14	32
0	47	25	2	3	4	15	33
-1	46	24	9	1	5	16	34
-2	45	23	8	7	6	17	35
-3	44	22	21	20	19	18	36

Fig. 4.3 Example of the hashing function assignment.

Individual cannot cross or if exclusion or competition prevents the individual from moving. After hashing is performed, a check is made to verify if any individual occupies a cell containing a barrier that he is not supposed to cross (with probability 1.0). If so, a warning is issued, indicating the conflict and the user is returned to EDIT to make the appropriate changes if desired.

4.2.5 COMPUTE

For each species, the user can specify a function of the current species size and current time step, to be applied at the end of every time step. A Fortran like expression has to be entered, as a function of x and t, like x**2 or x*(t+1). If the result is negative, deletions are made at random. If the population is to increase, additions of new individuals are made according to the initial distribution. COMPUTE is used first from CREATE to analyze the Fortran expression for correctness. After each time

step COMPUTE is called to execute the Fortran expression and determine how many individuals should be added or deleted.

4.2.6 RUN

RUN is the main simulation module, controlling the sequence of events in the system. A list is first established to define the order in which the species will be moved (by processing level). The number of time steps, output interval and halting conditions are then requested. For each species, an individual is found, at random, in the list (see Fig. 4.4) and a second random number determines the "direction" in which the list of individuals will be scanned. For each individual, the following sequence is executed:

1. Adjust the age of the individual
2. Move the individual if required
3. Let the individual eat, if required
4. Let the individual breed, if required.

After all individuals of a given species are processed, the global function of this species is applied if it exists. After all species are processed, a check is made to see if a species is out of bounds, i.e. if the number of individuals of a species is below the inferior limit or above the superior limit set by the user. If so, the simulation is stopped and control is returned to the MONITOR. The output interval is then checked, and output is produced if required.

4.2.6.1 MOVE

The mobility coefficient of the individual is determined according to the mobility variables a, b, c (see 4.2.2), the hunger level, and whether or not mobility is a function of hunger. A random number is picked up. If the individual is allowed to move, the following steps are executed:

1. Find in which cell the individual will move, according to the probabilities of the neighboring cells;
2. Check this cell to see if the individual is excluded, or if competition or a barrier prevents him from moving in this cell. He then dies and procedure KILL is used to delete the given individual from the data record;
3. If nothing impedes movement, move the individual by adjusting its coordinates and adjust minimum and maximum x and y if required.

4.2.6.2 EAT

If the predator is hungry (satiety level < satiety top), a check is made to see if any of the prey occupies the same cell as the predator. If not, the satiety level of the predator is decremented. If a prey occupies the cell and the predator did not reach the satiation level, or the maximum number of kills per unit time, the prey is eaten and the check in the cell continues until the predator has reached the satiation level or has killed the maximum number of prey.

4.2.6.3 BREED

According to the breeding probability, the number of offspring is first determined by generating a random number from a distribution $N(\mu,\sigma)$ where μ is the offspring mean and σ the offspring variance. For each of the offspring, a cell is picked at random around the parent and if competition, barrier, or exclusion characteristics of the cells occupants allow it, the offspring is "created" in this cell.

4.3 DATA STRUCTURES

The data structures are intended to save space and allow easy access and have been designed in accordance with the following constraints: species can move and grow without bound; editing can insert or delete whole components of a model in the middle of a simulation run; all members of a species must be found and processed at the same time; all organisms and objects in a given cell must be identified to determine if an organism can move there. Since only the last constraint suggests an array type organization, linked allocation of storage is the method of choice.

When a new species is introduced by the user, a record (called the SPECIES HEAD NODE) is created containing the general information pertinent to that species (see Fig. 4.4 and 4.7). A pointer allows access to the first species record and a pointer from species to species permits access to each of them as required. Individuals of each species are represented as a doubly linked circular list; an

individual node (IND. CELL NODE) carries the organism's location (coordinates), age, satiety level, and number of killed prey. A pointer to the species head node allows easy access to the general information about the species. The doubly circular linking allows control of systematic effects which might arise from always processing the individuals in the same order. Each time step, a random individual is chosen and the list is traversed in a randomly chosen direction, so that on the average each individual is processed before and after each other individual equally often.

Barriers are represented as singly linked location nodes (BARRIER CELL NODE) with pointers to a head node (BARRIER HEAD NODE) containing parametric barrier characteristics (see Fig. 4.5). A top node in the system contains pointers to the first nodes in the list which links the species head nodes and the barrier head nodes. Interspecies exclusion factors (EXCLUSION), predator characteristics (PREDATION), species/barrier specifications (SPEC/BARR) and stopping conditions (STOP COND) are maintained in separate lists.

The last data structure element is the hash table whose nodes head the linked lists of all organism and barrier nodes whose locations hash to that table entry. (see Fig. 4.6). Thus the last constraint mentioned above is satisfied. The hashing function is used each time an attempt is made to move an individual, to see if there is a

barrier affecting its mobility, or if exclusion or competition are relevant. Specific record contents are shown in Fig. 4.7.

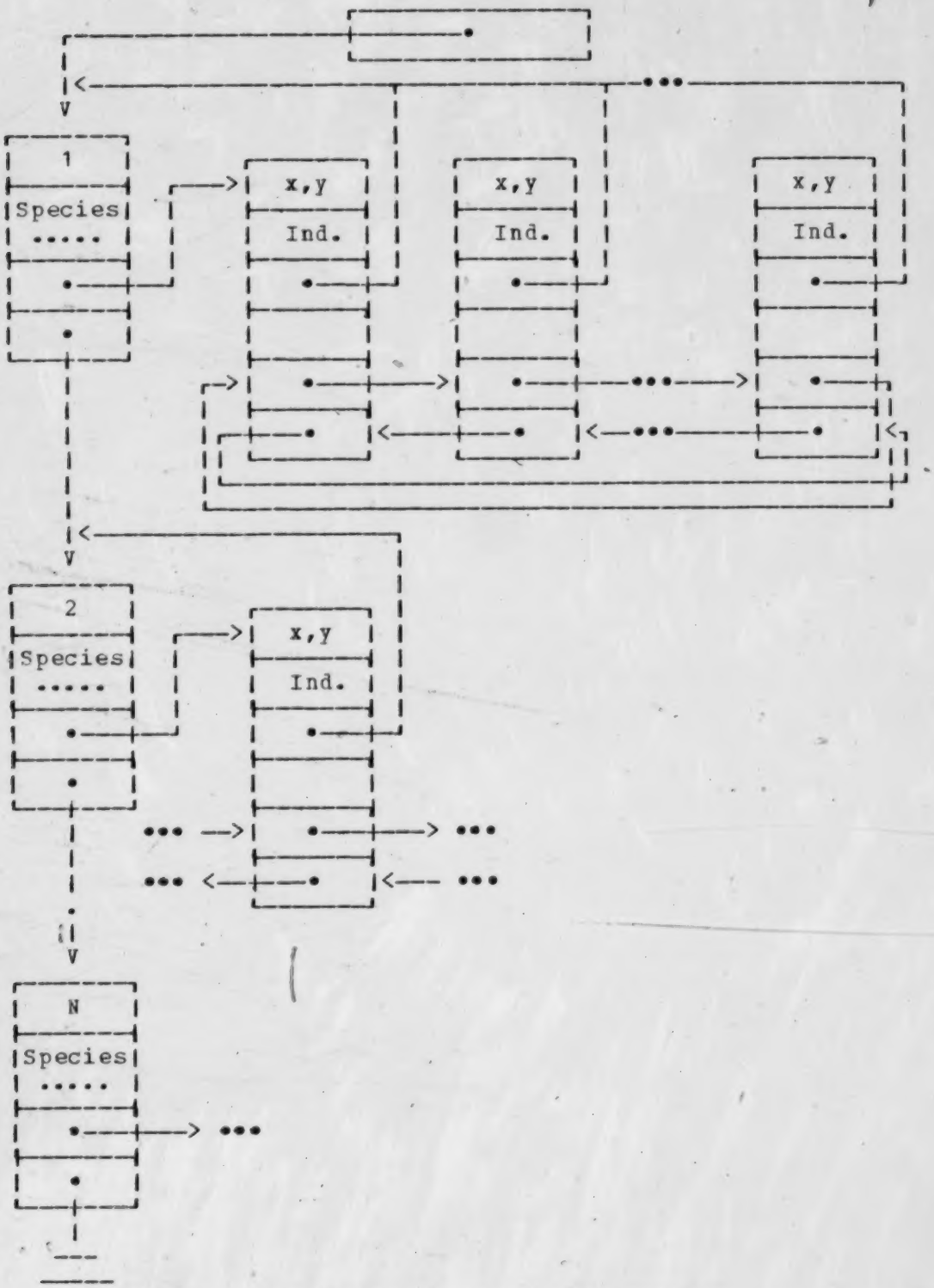

Fig. 4.4 Data structures for the species.

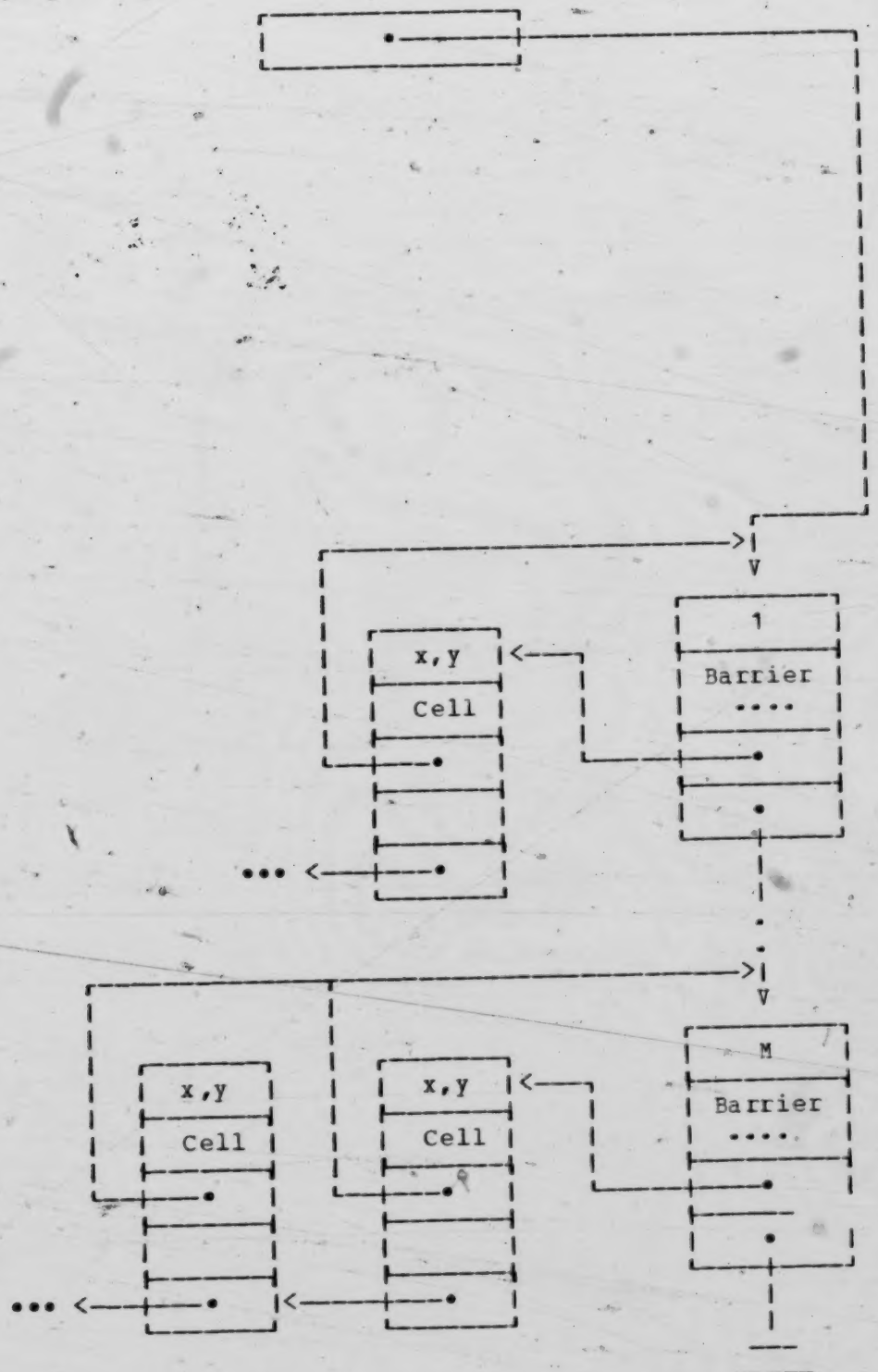

Fig. 4.5 Data structures for the barriers.

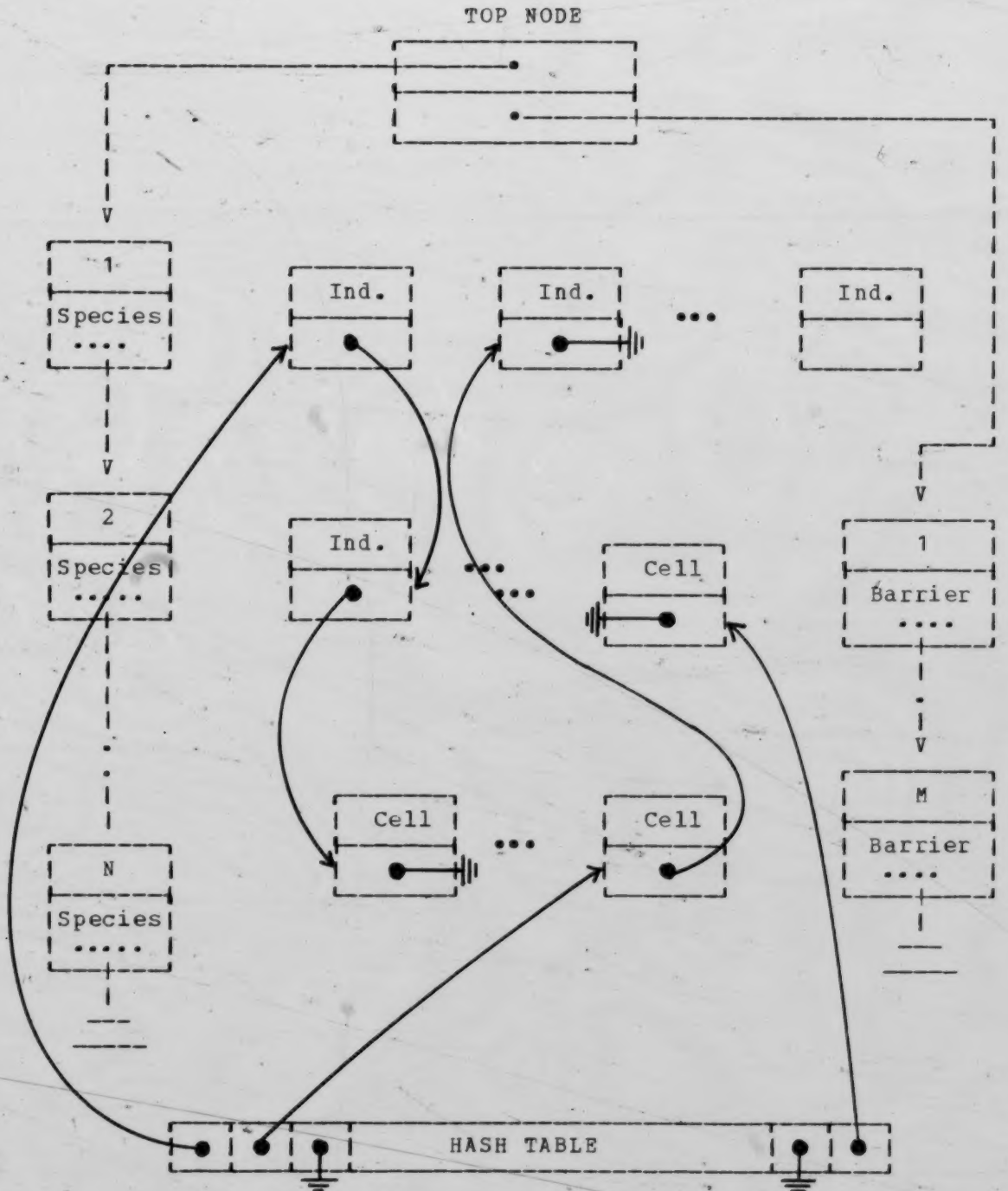

Fig. 4.6 Data structure with hash table.

Fig. 4.7 Node fields and other arrays.

CHAPTER 5

SYSTEM EVALUATION

5.1 APPLICATION: MURDIE'S MODEL

5.1.1 Background

ECOSIM is flexible enough to allow study of interesting ecosystems. Simulation runs can be carried out step by step, introducing features of the ecosystem gradually, to verify their effect on the model. The system studied here involves Murdie's (1971) experiments. He suggested that the spatial distribution of food or prey influences the ability of parasites and predators to successfully search for victims, and that predators show adaptive behavior in their searching patterns (see Section 3.2.2). After simulating an environment containing both clumped and non-clumped prey, Murdie concluded that clumped prey had a lower rate of predation than prey distributed at random, when predators moved by random walk.

Murdie distributed prey and predators in an environment represented by 150 independent quadrats of 10x10 cells each. All prey encountered were eaten except in certain runs where a satiation level of 10 prey was set. After twenty successive time steps without encountering a prey, a predator would die of starvation.

5.1.2 The Model

The model environment built using ECOSIM consisted of a 10x10 cell region corresponding to one of Murdie's quadrats. Various prey and predator densities were used. The prey were either distributed uniformily or clumped using a Normal distribution. Most of the time, the clump was placed in the middle of the grid, so that the "boxing-in" effect would be minimum at the physical limits of the region. The predators were distributed uniformily. A barrier rectangle was established around the region so that both prey and predators remained within the 10x10 area. To simulate Murdie's experiments, the prey were kept immobile while the predators moved by random walk (see Table 5.1, model type (1)). For some runs, a satiation level was set at 20 prey (Table 5.1, model type (2)), with starvation after 20 time steps without encountering a prey. Other features were then introduced like mobility of prey (type (3)), breeding characteristics for both prey and predators (not shown) and hunger dependent mobility for the predator (type 4)). Altogether, about 100 models were simulated, including some replications. A summary of results is shown in Table 5.1. A study involving refuge(s) for the prey was also performed.

5.1.3 Results

Most of the simulation runs were carried out for 100 time steps unless the predator or prey went extinct. In these cases, results were recorded at the time of extinction.

Reproducing Murdie's experiments could be done easily using ECOSIM except for the satiation level which had to be set at 20 instead of 10. Prey varied between 10 and 30 individuals and predators between 1 and 10. Some results were identical to Murdie's. For example, the number of prey killed was proportional to their initial number with both uniform and clumped distributions. Also, the introduction of a satiety level for the predator decreased the level of predation significantly. However, results indicate a higher level of predation when the prey were clumped, especially with a high prey density and when more than 1 predator was used. The fact that lower predation for clumped prey was observed in Murdie's experiments could be explained by the low density of predator in his studies. If a region contained only one or two predators, and these predators were placed at random, it could take a long time before they reached the prey area with a random walk search. Especially when starvation was introduced in the model, a predator could easily die before reaching the clump.

Table 5.1 Results of simulation experiments on Murdie-like models.

			RANDOM distribution		CLUMPED distribution	
model	number prey	number pred	number time steps	number prey killed	number time steps	number prey killed
	10	1	100	2	100	1
	20	1	100	4	100	3
(1)	10	10	56	10	52	10
	20	5	48	20	87	20
	20	10	52	20	57	20
	10	1	20	0	20	0
	20	1	55	2	20	0
(2)	10	10	49	9	28	4
	20	5	39	8	74	16
	20	10	38	16	29	20
	10	1	100	2	x	x
	20	1	100	6	x	x
(3)	10	10	47	10	x	x
	20	5	100	18	x	x
	20	10	100	19	x	x
	10	1	20	0	20	0
	20	1	26	1	33	1
(4)	10	10	40	7	46	9
	20	5	49	9	40	11
	20	10	61	15	73	17
	10	1	21	0	x	x
	20	1	91	14	x	x
(5)	10	10	20	10	x	x
	20	5	71	14	x	x
	20	10	63	19	x	x

(1) Simple model (like Murdie's): immobile non-breeding prey, mobile non-breeding predator
(2) Model with satiety (for predators):
satiation, starvation level : 20, 0
initial mean, var., +, - increment : 20, 0, 20, 1
(3) Mobility of prey, no satiety for predator
(4) Satiety and hunger dependent mobility for predators
(5) No mobility, satiety or breeding for prey, mobility, satiety and breeding for predator:
breeding int., prob., initial mean, var.: 5, 1, 1, 1
x : no experiment performed

When 5 or more predators were introduced, with no satiety characteristics, the prey species went extinct in an average of 59 time steps. A typical run is shown in Fig. 5.1. This surprisingly long period comes from the fact that if not enough prey were introduced, a predator could search for a long time before finding a prey. For some of the runs, 20 successive failures to find a prey led to the death of the predator. In all but one case, the predators went extinct before the prey after an average of about 38 time steps. The same results were obtained with the introduction of mobility for the prey (distributed at random).

When the mobility of the predator was made dependent on its satiety a slightly lower rate of predation was observed, especially for non-clumped prey, the predator staying for longer periods in "empty" areas.

Interesting results were obtained by introducing breeding, first for the predator only and then for both the prey and the predator. In the first case, the predator species went extinct, after an increase to about 30 individuals (from 10 initially), despite the breeding, mostly because of an insufficient number of prey (see Fig. 5.2). But in the second case, coexistence was achieved for at least 100 time steps, with both predator and prey in sufficient number. Values for the breeding characteristics were identical for the prey and the predator: a breeding interval of 5, a breeding probability of 1.0, and an

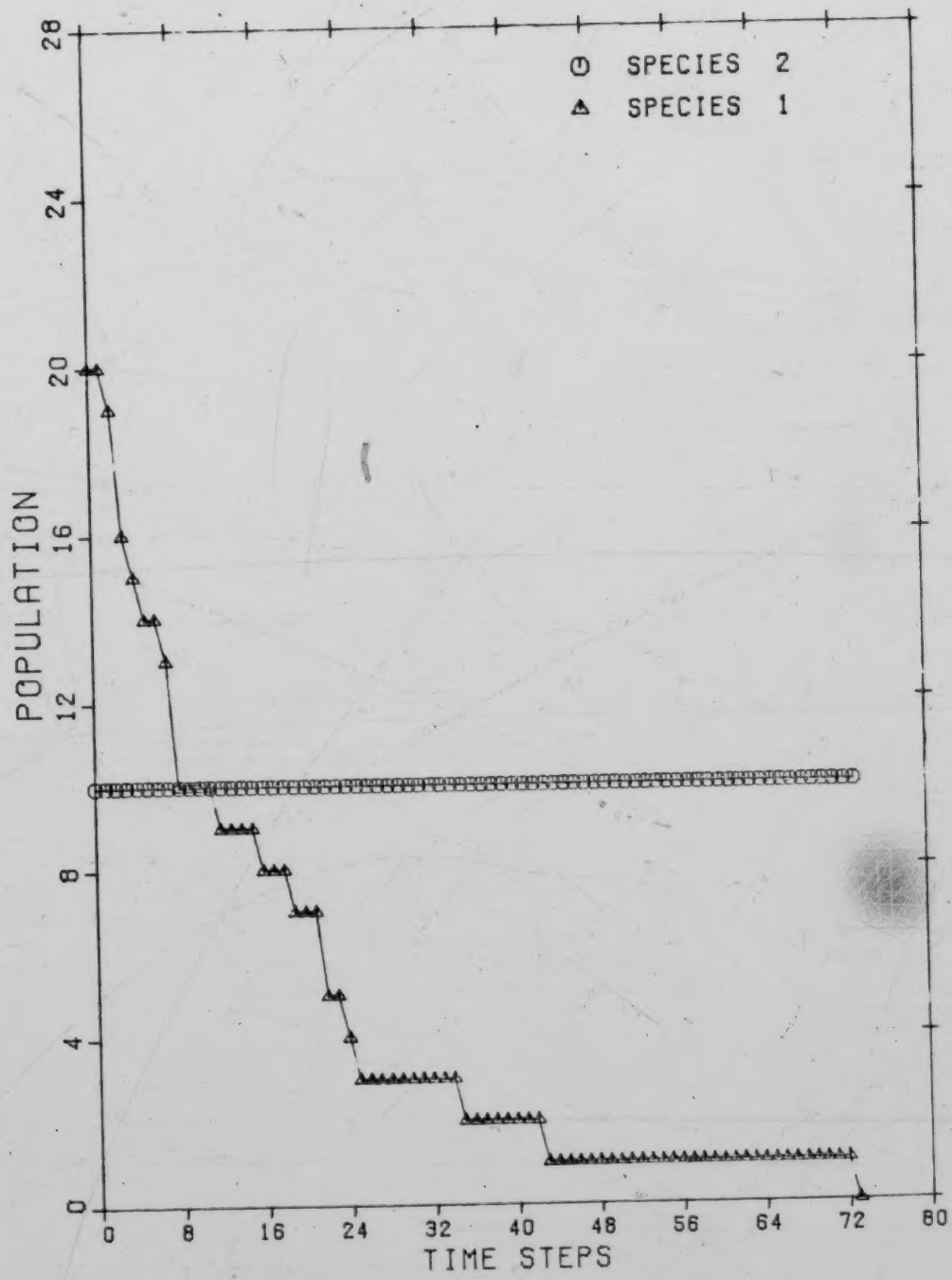

Fig. 5.1 Simple model without satiety for prey
(species: 1-prey, 2-predator)

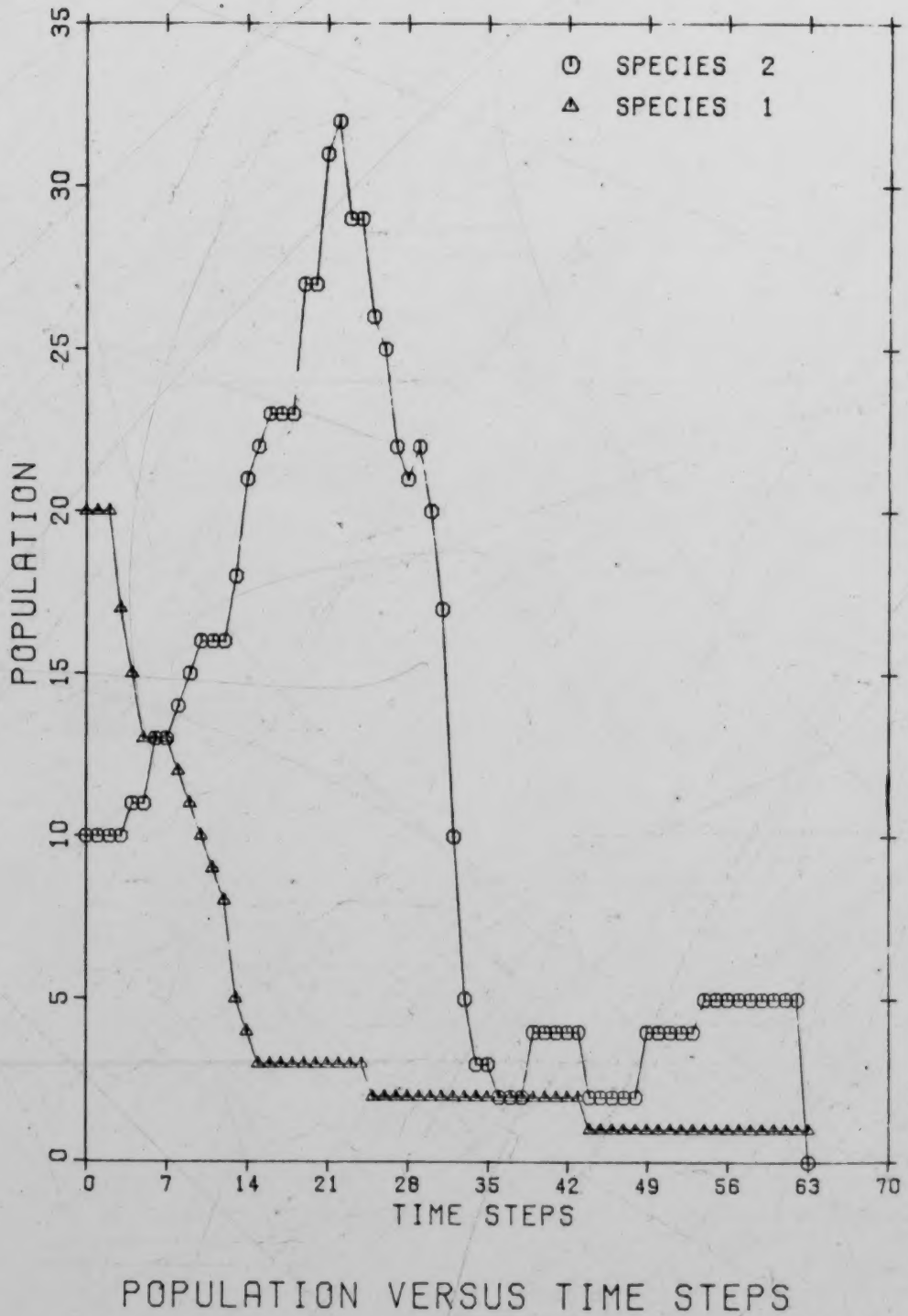

Fig. 5.2 Breeding for predators only
(species: 1-prey, 2-predator)

offspring distribution of N(1,1). With an initial environment of 10 prey and 1 predator, 27 prey and 76 predators existed after 100 time steps. It is likely that the predators would have taken over and annihilated the prey and then starved, but increasing the breeding values for the prey could lead to coexistence (see Fig 5.3).

With the introduction of refuges for the prey, chances of coexistence increased. A system of type (3), with 20 prey and 5 predators was run for 150 time steps without the extinction of the prey despite the fact that no breeding was introduced (see Fig 5.4). In this case, the refuge was made of 30 cells in the middle of the grid. When 5 small refuges of 6 cells each were introduced, the prey died faster than with one refuge, mainly due to the fact that a refuge would usually have a predator nearby.

5.2 SYSTEM REQUIREMENTS AND PERFORMANCE

ECOSIM is written in ALGOLW, a revised version of a language designed at Stanford University. The ALGOLW compiler is available under the Michigan Terminal System (MTS) at the University of Alberta. MTS is a virtual memory, multi-task system developed at the University of Michigan to support both on-line and batch jobs. It runs on an Amdhal 470V/6 at the University of Alberta. A paging system is used for memory management. Other features of MTS include the supervisor which handles scheduling and resource allocation, Device Support Routines, and a spooling

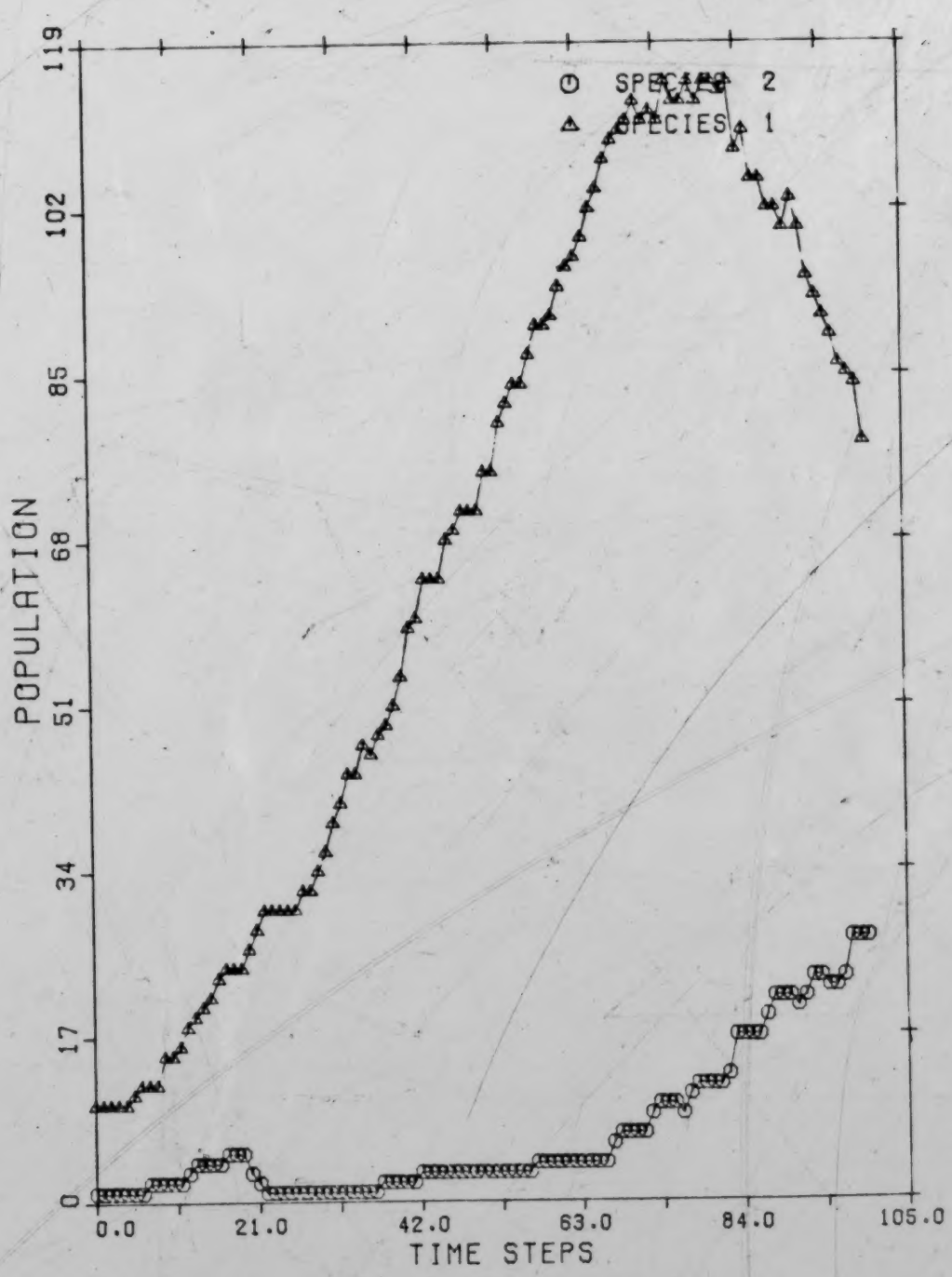

Fig. 5.3 Breeding for both prey and predators
(species: 1-prey, 2-predator)

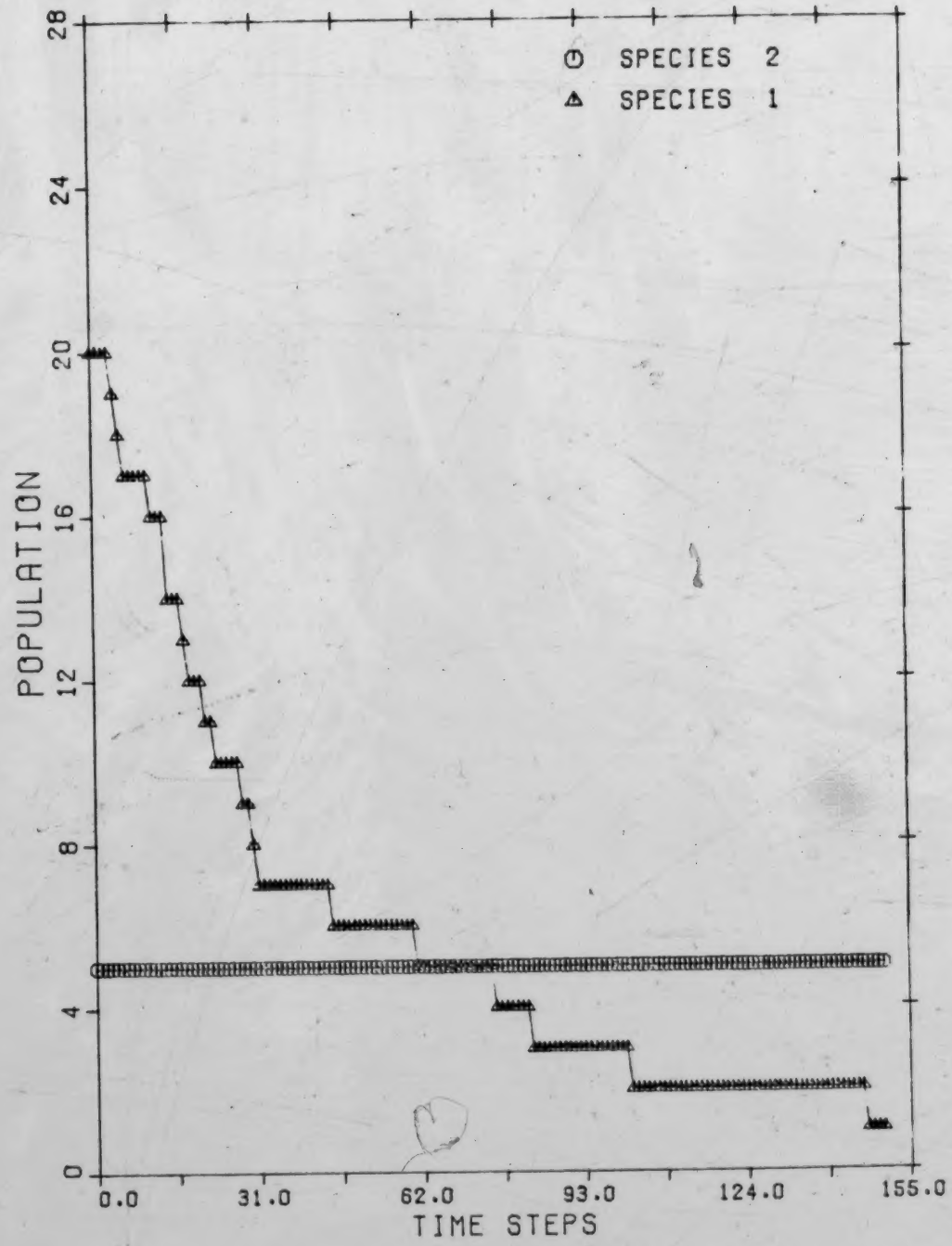

Fig. 5.4 Introduction of refuges
(species: 1-prey, 2-predator)

subsystem (HASP) which handles I/O operations.

ECOSIM uses 90 4096-byte pages of memory during compilation, and the object file can be stored in a file of 3224 lines. It takes approximately 8 seconds to compile the program, depending on the computer load.

Parts of the program are written in FORTRAN and ASSEMBLER. Most of the FORTRAN routines are system routines used to interface with MTS. The random number generator was written in ASSEMBLER using a version created at the University of British Columbia.

The response time of ECOSIM is fast, despite the extensive dialogue designed for the novice user. Except when a large number of species is involved, or if the output interval is quite large, ECOSIM responds virtually instantaneously.

When ECOSIM is run, 10 pages of memory are allocated by default. If the user is planning to create more than 800 individuals or 1000 barrier cells, he should increase the number of pages to be allocated.

It takes on the order of one tenth millisecond of CPU time to create a barrier cell and one millisecond to create an individual of a species. To process 1 mobile individual for 1000 time steps takes approximately 1.4 seconds. A complete system of 10 mobile breeding prey individuals and 10 mobile breeding predators with satiety characteristics is processed in about 1/4 CPU second per time step. More time is required when involved output is produced.

ECOSIM is somewhat dependent on the MTS system for certain I/O routines and would require minor modifications to be made portable, but could be adapted to many large computer systems having ALGOLW compilers.

5.3 CONCLUSION

ECOSIM is designed to provide a useful and easy tool for ecological modeling. An involved dialogue provides the interactive facility needed for the model definition and the monitoring of the simulation. Realistic environments can be simulated with the many available parameters, and even unrealistic studies can be done to discover the effect of parameter variations.

ECOSIM could be improved in several ways. First, the environment is uniform. Each cell is identical except for the inclusion of individuals and barriers. No "physical" variables characterize the environment, like the moisture of the soil or the temperature. The individuals, as they exist in the system, are not distinguished by sex. Breeding specifications for a given species apply to all individuals. Thus all individuals are "female". Mating is not included in the system. Breeding is done at regular intervals whether or not an individual is alone. No age structure is included. An individual will not die or reproduce according to its age but according to the global function, predation and breeding variables. A function could be introduced and checked so that reproduction could be made dependent on age

and so that individuals would die accordingly.

Finally, predators do not seek prey. In the system design, it was assumed that a cell is the physical immediate environment of an individual, as far as it can see and predate in the time step.

The use of computers for simulation in community ecology is an enterprise still in its infancy. It may be hoped that availability of general purpose simulation systems like ECOSIM will advance both the study of ecology and the art of simulation.

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APPENDIX

USER'S MANUAL

A.1 INTRODUCTION

Before looking at the conversation between ECOSIM and the user, the procedure to use ECOSIM and the general constraints of the system are given. ECOSIM is easy to use and error recovery is simple. Most of the time, the question is repeated until a valid answer is given. If the situation is ambiguous, the error is pointed out so that the user can correct it.

A.2 GENERAL NOTES

In the following, computer entries are in capital letters while user's entries are in lower case letters. The procedure to run ECOSIM is as follows:

```
# signon i.d.
# PASSWORD?
? password
# TERM ...
# **LAST SIGNON ...
# USER "I.D."  ...
# $run mimi:ecosim t=(number of seconds desired)
```

From then on, the user supplies answers to questions. Restrictions about the answers are as follows:

1. No answer should exceed 20 characters. Additional characters will be ignored.
2. No more than two numbers can be given at one time. Additional numbers will be ignored.
3. Integers must be between -2147483648 and 2147483647.

4. Absolute values of reals must be between 5×10^{-79} and 7×10^{75}.
5. When a question ends with a question mark, the user can answer by YES, Y, NO, or N.
6. Some answers must be integers (like coordinates). The question will be repeated if a real is given.
7. When an answer should be a real, an integer is considered valid (the decimal point is not necessary).
8. If a pair of numbers is requested, they must be separated by a blank. These numbers will always be integers.
9. A temporary file is created at the beginning of the run, and all the information about the state of the model is stored. At the end of the run, the user has the choice of making the file permanent and/or printing the result at the batch printer.
10. If plotting is requested, the user has to execute an extra step after the run is complete:

    $RUN *CALCOMPQ PAR=FILE=-PLOT

    The user is then informed of the cost of the plot and asked if he still wishes to get it. If YES, a receipt number is issued and the plot can be picked up later.
11. If the user is planning on creating a big environment, he should specify PAR=SIZE=##P on the RUN command, where ## is the number of pages required. The default option is 10 for about 800 individuals.

A.3 CONVERSATION

In what follows, YES means YES or Y, NO means NO or N and REAL means a real number with or without a decimal point.

EXPLAIN?.....YES OR NO

If the answer is YES, the user is given a resume of the features of the system.

CREATE?.....YES OR NO

If the answer is YES, the user will be asked a series of questions about the model he wants to create. If the answer is NO, a filename is requested to retrieve an existing model.

DESCRIBE ENVIRONMENT?.....YES OR NO

If the answer is YES, the user is given a resume of the characteristics of each species and barrier and each individual of the different species and barriers at the terminal.

EDIT, SAVE, QUIT, OR RUN?.....E, S, Q, OR R

If the answer is E (or EDIT), a series of questions is generated to execute the required changes.
If the answer is S (or SAVE), the user is asked for the name of a file which is created, and the current state of the model is stored for further use. The different variables are stored in a compact form not readily readable from the file. The file name is given the prefix of USER. So that the user can recognize the files he created during the run. For example, if the user creates a file name WORLD1 the real file name will be USER.WORLD1 but if the file name is requested (for retrieving information), the modeler uses the name he gave to the file i.e. WORLD1.
If the answer is Q (or QUIT), the user is asked if he wants the temporary file containing the information about the run to be made permanent. If yes, a file name is requested and saving is attempted. The user gets another chance if the file exists already or the name given is illegal but not if there is not enough disk space to save the file.
If the answer is R (or RUN), the simulation is initiated with the current state of the model (newly

created or retrieved from a file).

EDIT, SAVE, QUIT, OR CONTINUE?.....E, S, Q, OR C

Same as the previous question for E, S, and Q. If the answer is C, the simulation is resumed where it was halted with all parameters preserved.

RUN COMPLETE. RESULTS DESIRED?.....YES OR NO

If the answer is YES, a list of all species and barriers with their characteristics and the characteristics of each individual is given.

SPECIES N?.....YES OR NO

If the answer is YES, species number N will be created (questions will be asked about its characteristics). If the answer is NO, questions about the barrier(s) to be created will be initiated.

DISPLAY SYMBOL:.....1 CHARACTER

Any character except % is valid to represent a species or barrier. When the environment is displayed, each individual of the given species or barrier is represented with this symbol.

PROCESSING LEVEL:.....INTEGER

A positive integer is requested. Motile species with the lowest processing level move first.

MOBILITY(0-1):.....REAL

A number between 0 and 1 (inclusively). If mobility is 0, the individuals of the species never move. If mobility is 1, each individual will attempt to move at every time step. If mobility is for example 0.8, the probability of each individual of the species to move at every time step is 0.8.

COMPETITION FACTOR(0-1):.....REAL

A number between 0 and 1 (inclusively). This is requested only if the species is motile. A competition factor of, say 0.6, means that if an individual attempts to move in a cell that another individual of the same species occupies, he will "die from competition" with a probability of 0.6.

UNIFORM RANDOM WALK?.....YES OR NO

This is requested only if the species is motile. If the answer is YES, a probability of 1/7 is assigned to each of the seven variables representing the six cells around and the cell occupied by the individual.

6 WALK. PROB. (CLOCKWISE FROM UPPER RIGHT)....6 REAL NUMBERS

This is requested only if the species is motile. Each real number (between 0 and 1) must be on a new line. If the given probabilities are a, b, c, d, e, and f, they are assigned clockwise from upper right (see Fig. A. 1). The center cell (g) is assigned a probability of 1-(a+b+c+d+e+f).

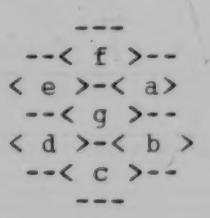

Fig. A.1 Assigned probabilities for random walk.

If a given number is invalid, the user is requested to reenter it. If the total of the six probabilities given exceeds 1.0, the user is asked to reenter all six probabilities.

PREDATOR?.....YES OR NO

If the answer is YES, the user will then enter the predator characteristics of the species. If the answer is NO, the given species will not have predator, breeding and hunger characteristics.

PREY SPECIES:.....INTEGER OR NOTHING

A positive number or null line. If an integer is given, a table is created containing the predator number and the prey number. When all prey species have been specified for the given predator, the user continues by entering a null line.

PROBABILITY OF KILLING:.....REAL

A number between 0 and 1 (inclusively). The number denotes the probability that the predator will kill the prey if he encounters one.

MAX KILLS / UNIT TIME:.....INTEGER

A positive integer which indicates the maximum number of prey that the predator can kill during one time step.

BREEDING INTERVAL:.....INTEGER

A positive integer giving the interval (in time units) between breeding events for this particular species. The initial age of the individuals are distributed uniformily over the age interval.

BREEDING PROBABILITY:.....REAL

A number between 0 and 1 indicating the probability of a breeding event when the breeding event time is reached.

OFFSPRING MEAN:.....REAL

A real number representing the mean of a Normal distribution used to determine the number of offspring to be created.

OFFSPRING VARIANCE:.....REAL

A real number giving the variance of the Normal distribution used to determine the number of offspring to be created.

SATIETY SCALE TOP:.....REAL

A real number indicating the satiation level of the species. If the satiety level of an individual is equal to the satiety scale top, he does not eat even if he encounters prey.

SATIETY SCALE BOTTOM:.....REAL

A real number less than the satiety scale top representing the starvation level of the species. If the satiety level of an individual is less than or equal to the satiety scale bottom, the individual dies.

+ INCREMENT:.....REAL

A real number which is added to the hunger level each time an individual of the given predator species eats a prey. The hunger level does not exceed the hunger scale top for the species.

- INCREMENT:.....REAL

A real number which is subtracted to the hunger level each time an individual of the given predator species eats a prey.

SATIETY INITIAL MEAN:.....REAL

A real number representing the mean of a Normal distribution used to determine the initial hunger level of each individual of the given species.

SATIETY INITIAL VARIANCE:.....REAL

A real positive number giving the variance of the Normal distribution used to determine the initial hunger level of each individual of the given species.

SATIETY DEPENDENT MOBILITY?.....YES OR NO

If the answer is YES, the probability of moving for an individual at a given time step is determined not only by his mobility factor but also by his hunger level. The probability value f(x) will be on the curve passing through (0, HUNTOP), (MOB.COEFF., (HUNTOP+HUNBOT)/2), and (1, HUNBOT) where x is the hunger level of the individual, HUNTOP and HUNBOT are the hunger top and bottom, and MOB.COEFF is the mobility coefficient of the individual.

EXCLUSIONS?.....YES OR NO

If the answer is YES, the user is asked which species are excluded i.e. which species' individuals cannot move in a cell occupied by an individual of the given species.

SPECIES NUMBER:.....INTEGER

An integer greater than 1 specifying the species to be excluded by the active species. When no answer is given (null line) it is assumed that no other species is excluded.

INITIAL NUMBER:.....INTEGER

A positive integer representing the initial number of individuals to be created.

RANDOM DISTRIBUTION?.....YES OR NO

If the answer is YES, individuals or barrier cells are distributed according to a random distribution (chosen by the user after); if the answer is NO, specific coordinates will be requested.

U, N, E, OR P:.....1 CHARACTER

The answer should be the character U, N, E, or P. If the answer is U, the individuals or barrier cells are distributed according to a Uniform distribution in X and a Uniform distribution in Y (parameters are requested subsequently). If the answer is N the distribution used is Normal, if E, Exponential, and if P, Poisson.

X(Y)NMEAN:.....REAL

A real number representing the mean of the Normal distribution of the X(Y) coordinates.

X(Y)NVAR:.....REAL

A positive real number representing the variance of the Normal distribution of the X(Y) coordinates.

X(Y)NLIMINF(SUP):.....REAL

A real number indicating the limit for rejecting values generated according to the Normal distribution.

X(Y)MIN:.....REAL

A real number indicating the minimum value for the X(Y) coordinates of the individuals distributed uniformly.

X(Y)MAX:.....REAL

A real number > X(Y)MIN indicating the maximum value for the X(Y) coordinates of the individuals distributed uniformily.

XELAMB:.....REAL

A real number giving the value of lambda in the exponential random distribution.

XEORIG:.....REAL

A real number indicating the origin of the exponential curve.

XELIMIT:.....REAL

A real number indicating the limit for rejecting values generated according to the exponential distribution.

The following variables are similar to the previous ones, but apply to different distributions:

YELAMB, YEORIG, YELIMIT, XPLAMB, XPORIG, XPLIMINF,

YPLIMSUP, YPLAMB, YPORIG, YPLIMINF, YPLIMSUP

N X-Y COORDINATE PAIRS:.....N INTEGER PAIRS

N integer pairs should be entered, one pair per line, indicating the positions of the grid in which the N individuals are to be placed. Or, the user can enter $CONTINUE WITH FILE RETURN, where FILE contains the given number of coordinates, one pair per line, each number separated by a blank.

PRINT INITIAL DISTRIBUTION?.....YES OR NO

If the answer is YES, the distribution of the individuals is listed in the form of a table giving, for each individual, its position (X,Y), its age, its hunger level, and the number of prey killed.

GLOBAL MODIFICATIONS?.....YES OR NO

If the answer is YES, a function is then requested that is applied to the population of the given species at every time step. If the applied function implies a decrease in the population, individuals are deleted at random. If the result is an increase, individuals are created according to the initial distribution for position and hunger level.

FUNCTION:.....UP TO 80 CHARACTERS

A string representing a function of X where X is the present population (number of individuals). For example X-2 or 2+(X**2). The string should not contain intervening blanks as a blank indicates the end of the string.

BARRIER N?.....YES OR NO

If the answer is YES, barrier number N is created (questions are asked for characteristics). If the answer is NO, creation of the model is considered complete.

SPECIES:.....INTEGER OR NOTHING

A positive number 0 or nothing (simply press ENTER). If an integer is given, a table is created containing the barrier number and the species number. When all species numbers have been specified for the given barrier, the user enters a null line.

CROSSING PROBABILITY:.....REAL

A number between 0 and 1. The number denotes the probability that the species individual will cross the barrier if he encounters one.

NUMBER OF CELLS:.....INTEGER

A positive integer representing the initial number of individual barriers to be created.

SPECIFIC (S), OR CORNERS (C):.....S, OR C

The user has the choice of specifying the barrier cells one by one or by giving the coordinate of the four sides of a rectangle (left, right, top, bottom).

LEFT (RIGHT, TOP, BOTTOM):.....INTEGER

The left (right, top, bottom) coordinate of the rectangle formimg the barrier has to be specified.

FILENAME:.....UP TO 20 CHARACTERS

A file name has to be given. If the user requests an environment previously saved on file, the file must exist. If the file name is requested to store an environment or the results of a run, the file must not exist and is created by the system.

TRY ANOTHER FILE?.....YES OR NO

This question comes if an attempt is made to create a file which already exists or to get a file which does not exist. If the answer is YES, a second attempt is made.

EDIT BARRIER, SPECIES, OR END:.....B, S, OR E

If the answer is B, the user is asked to enter information about the barrier he wants to edit. If the answer is S, species editing is initialized. If the answer is E, editing is terminated.

ADD, DELETE OR MODIFY A SPECIES:.....A, D, OR M

Depending whether the answer is A, D, or M, questions are asked to create, destroy, or modify a species.

WHICH SPECIES:.....INTEGER

If the answer to the previous question is D or M, the user is asked to specify the species (positive integer).

MODIFY:
...DISPLAY SYMBOL?.....YES OR NO

If the answer is YES, the user is prompted for a new display symbol.
For the following, if the user answers YES, he is prompted for the change.

...PROCESSING LEVEL?.....YES OR NO

...MOBILITY FACTOR?.....YES OR NO

...COMPETITION FACTOR?.....YES OR NO

...WALKING PROBABLITIES?.....YES OR NO

...PREDATOR CHARACTERISTICS?.....YES OR NO

...MAX KILLS / UNIT TIME?.....YES OR NO

...PROBABILITY OF KILLING?.....YES OR NO

...BREEDING INTERVAL?.....YES OR NO

...BREEDING PROBABILITY?.....YES OR NO

...OFFSPRING MEAN?.....YES OR NO

...OFFSPRING VARIANCE?.....YES OR NO

...SATIETY TOP?.....YES OR NO

...SATIETY BOTTOM?.....YES OR NO

...HUNGER MOBILITY FUNCTION?.....YES OR NO

...+ INCREMENT?.....YES OR NO

...- INCREMENT?.....YES OR NO

...EXCLUSION CHARACTERISTICS?.....YES OR NO

...GLOBAL FUNCTION?.....YES OR NO

...PREY SPECIES?.....YES OR NO

...INDIVIDUALS?.....YES OR NO

...SPECIES/BARRIER CHARACTERISTICS?.....YES OR NO

...COORD. (C), SATIETY (S), OR BREEDING (B):.....C, S, OR B

Depending on the answer, the coordinates of an individual are altered, or his satiety level or his age.

DOES SPECIES N BECOME A PREDATOR?.....YES OR NO

This information is requested if the user asked to change the predator characteristics and the given species was not a predator before.

DOES SPECIES N REMAIN A PREDATOR?.....YES OR NO

This information is requested if the user asked to change the predator characteristics and the given species was already a predator.

CHANGE, DELETE OR ADD:.....C, D, OR A

If the answer is C, changes to existing prey species are initiated. If the answer is D, species N will no longer be a predator for the species specified. If the answer is A, a new record is created since species N will now prey on a new species.

ADD, DELETE, OR MODIFY INDIVIDUALS:.....A, D, OR M

Depending whether the answer is A, D, or M, questions will be asked to create, delete or modify individuals. "Individuals" here is taken as an individual of a species or an individual barrier cell.

HOW MANY:.....INTEGER

A positive integer specifying how many individuals are to be created, deleted or modified (depending on the previous answer).

GIVE A COORDINATE PAIR:.....INTEGER PAIR

A coordinate pair has to be given indicating the position to add, delete, or modify the individual. If the user does not remember the existing individuals' positions, he can press END OF FILE. A listing of the position of each individual will be given so that when the user is reasked the question "...INDIVIDUALS?", he knows where to delete or modify them.

NEW COORDINATES:.....INTEGER PAIR

This new coordinate pair becomes the new position of a "modified" individual.

ADD, DELETE, OR MODIFY A BARRIER:.....A, D, or M

Depending whether the answer is A, D, or M, questions are asked to create, delete or modify a barrier.

WHICH BARRIER:.....INTEGER

If the answer to the previous question was D or M, the user is asked to specify the barrier (positive integer).

UNTIL WHICH TIME STEP:.....INTEGER

An integer number specifying until which time step the run is to be carried.

OUTPUT INTERVAL:.....INTEGER

An integer number indicating the output interval for which the environment can be displayed.

STOPPING CONDITIONS: SPECIES.....INTEGER

An positive integer specifying for which species do stopping conditions exist.

MIN, MAX:.....INTEGER PAIR

An integer pair giving the bounds on the population of the given species. If the number of individuals of this species becomes less than MIN or more than MAX, the simulation run is halted.

RESULT FILE TO BE MADE PERMANENT?.....YES or NO

If the answer is YES, the temporary file which contains all the results of the simulation run is renamed to be made permanent. A filename is requested.

PRINT RESULT FILE?.....YES or NO

If the answer is YES, the file containing the result of the simulation run is printed at a batch printer and a receipt number is issued.

PLOT?.....YES or NO

If the answer is YES, species numbers are requested. For each species, population versus time step is plotted on the Calcomp plotter. All species are plotted on the same graph. The user can separate the plots on different graphs by answering YES to successive "PLOT?"s. At the end of the run, the user should

$RUN *CALCOMPQ PAR=FILE=-PLOT

if he wishes his plots to be executed.

MAXIMUM SIZE OF GRID:.....INTEGER

An integer between 1 and 16 indicating tha X and Y dimension of the grid (number of cells horizontally and vertically). A size of 14, for example, will create 14x14 windows.

GRID (G) OR NO GRID (N):.....G or N

If the answer is G, a grid is drawn around the individuals when the state of the model is displayed. If the answer is N, only the contour of the given state of the model is drawn.

DISPLAY OUTPUT?.....YES or NO

At each time where the output interval is reached, the user has the option of cancelling the display of the state of the model on the terminal (the state of the model is still recorded in the temporary file).

PEGION:.....INTEGER

The state of the model environment is divided into up to 16x16 cells. The region numbers run horizontally. The user sees only the desired regions on the screen.

STATISTICS?.....YES OR NO

If the answer is YES, statistics are given about every species and every barrier for the present state of the model.